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As the Nation's principal conservation agency, the Department of the Interior has basic responsibilities for water, fish, wildlife, mineral, land, park, and recreational resources. Indian and Territorial affairs are other major concerns of America's "Department of Natural Resources."

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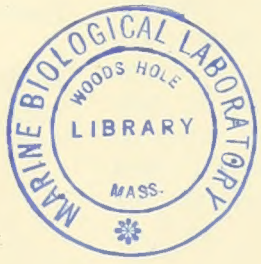

MARINE DECAPOD CRUSTACEANS OF THE CAROLINAS

By Austin B. Williams

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INTRODUCTION

Knowledge of the crustacean fauna of the Carolinas has grown slowly over many decades. Early in the last century, Thomas Say described species from the Carolinas, and in the middle 1800's Professor L. R. Gibbes, who maintained a private collection in Charleston, S.C., described species from the Carolinas. William Stimpson (1860b), who visited Beaufort, N.C., in company with T. N. Gill, gave a list of 38 species of decapod crustaceans which he collected there. Elliott Coues (1871), at that time an Army surgeon stationed at Fort Macon, N.C., recorded 27 species of decapods from the Beaufort area, 8 of which were additions to Stimpson's list. Seven years later, Coues and Yarrow (1878) gave a list of six species, two of which had not appeared previously. An appendix to the same paper by J. S. Kingsley included 51 species from the Beaufort area, and 3 of these were additions to the fauna. A year later, Kingsley (1879) contributed eight more new records.

The collection which was the subject of Kingsley's report had been made by Professor H. E. Webster, of Union College. It was later transferred, in part at least, to the U.S. National Museum, and supplied the types of *Lepidopa websteri* Benedict and *Pinnixa cristata* Rathbun, both collected near Beaufort, N.C.

Professor W. K. Brooks and his students, of the Johns Hopkins University, studied crustaceans at Beaufort at intervals from 1880 to 1903. They contributed information on habits and development, but only one or two new species were added to the faunal list.

Shore's manuscript included 87 species, but he omitted 8 which had been listed by the writers already mentioned. He had added 33 species, making a total of 95 species for the region.

Following this, exploratory work on offshore fishing banks by the *Fish Hawk* in the summers of 1914 and 1915, energetic shore and shallow-water collecting by parties from the Bureau of Fisheries laboratory at Beaufort, and inclusion of freshwater species from the region, enabled Hay to add 57 species to Shore's list. These, plus description of a new species by Rathbun, brought the total number known from Beaufort, N.C., in 1918 to 153 species.

The authors pointed out that some of these species had not yet been reported from the area, though from distribution elsewhere they might be expected. Also, some of the species were considered more properly to be deep-sea forms, rather than strictly members of the Beaufort fauna, although they had been found on the continental shelf not far distant.

In the year the handbook appeared, Mary J. Rathbun brought out the first in a series of four monographs on recent crabs of the Western Hemisphere, and, thus, began a new advance in knowledge of Carolinian crustaceans, later furthered by major revisions of the Penaeidae by Burkenroad, revisions of Hippolytidae, Palaemonidae and Scyllaridae by Holthuis, Galatheidae by

Note.—Approved for publication May 25, 1964.

Chace, Paguridae by Wass, Thalassinidea by de Man, Oxyrhyncha by Garth, and the Porcellanidae by Haig. Schmitt's treatment of the Macrura and Anomura of the Puerto Rican area, as well as his contributions on the Hippidae and the genera *Callianassa* and *Upogebia*, and Verrill's completion of the work on Bermudan decapods added breadth to knowledge of distribution as well as taxonomic stability. Closer at hand, the studies of Lunz in South Carolina yielded similar results. To this list of scholars could be added the names of Borradaile, Glassell, and Provenzano, who described new forms from the Carolinian province. The works of these and other authors are given in detail in the text to follow.

Apart from these primarily systematic studies, a growing number of ecological studies have been published during the past 45 years. Such results are not usually cited in systematic handbooks, but because this one is directed primarily to students and ecologists who are often newcomers to the area, brief summaries have been attempted. The review of literature, though not complete, is exhaustive enough to lead to most of the published material.

Actually, few species have been studied in detail. Of these, almost all are littoral species easily accessible to the investigator by virtue of their abundant numbers and ecological niches. Beyond this, a few species of commercial value such as *Callinectes sapidus* and *Penaeus* spp. have been studied in detail. It is fair to say that ecological studies are scarcely started.

SYSTEMATIC DISCUSSION

This is a review of published material. Arrangement of families and genera follows that adopted by the most recent reviser of each group. Important diagnostic characters of families and genera have been incorporated in keys and are often repeated, in part, in species descriptions. Brief diagnoses of families are included to aid in identification. Diagnoses of genera are not included, with some exceptions, for these exist in the literature. Such treatment leads to repetition but gives more complete descriptive accounts for individual species.

The general key to suborders, sections, superfamilies, and families serves as a rough index, and an attempt has been made to arrange it "phylogenetically". Other keys to subfamilies, genera, and species are either combined or separate depending on number of genera or species involved, and these keys are scattered throughout the text.

There is a tendency in carcinology to assume a specialized background on the part of readers, and beginners may find themselves troubled with terms. A number of monographs have included introductory glossaries and figures with detailed labeling as aids, but these are not always adequate because terminology in various suborders and sections lacks consistency.

An illustration of inconsistency follows: Among shrimps, the pereiopods are often called the first, second, third, fourth, and fifth walking legs. Among crabs, the tendency is to call the first pereiopods, chelipeds, because they are almost invariably larger than the remaining legs and are the only chelate pair (except in anomuran and some dromiid crabs). The remaining pereiopods are then termed the first, second, third, and fourth walking legs. This inconsistency seems firmly entrenched and it is based on functional morphology, the shrimps tending to have five pairs of legs functionally adapted to walking, but most crabs only four. Because many shrimps do not walk, legs in this group herein have been called "legs," the term "walking legs" being reserved for crabs. Hopefully, the use of explanatory figures adapted from existing works, together with the glossary, will resolve most of such difficulties

In the species accounts, no attempt has been made to include complete synonymies. A great deal of spadework by recent specialists has made abbreviation of synonymies desirable and practical; therefore, most are restricted to citation of original description, Hay and Shore (where applicable), and work of the most recent reviser.

Many descriptions which Hay and Shore wrote have been paraphrased, and many measurements, descriptions of color, and ecological notes have been included essentially unchanged. When available, more recent information has been used, and for this I have depended heavily on Rathbun (1918b, 1925, 1930a, 1937), Schmitt (1935a), and Holthuis (1951a, 1952, 1959) for key characters, color notes, and depth and latitudinal ranges. For these works, specific citations in the text have often been excluded for the sake of brevity.

ZOOGEOGRAPHIC CONSIDERATIONS

Though the original title implied a local list, the handbook included an assemblage that is quite widespread. Hay and Shore justly termed it a virtual descriptive list of decapod crustaceans of the Middle Atlantic coast, in large measure filling but continuing in part from northwestern Florida the gap between various lists of New England, New York, and New Jersey crustaceans, and the Puerto Rican list (Rathbun, 1901). The assemblage treated, both by Hay and Shore (in the original) and this revised version, has a latitudinal range extending primarily from Cape Hatteras, N.C., to northeastern Florida (fig. 1), to Texas; it is encompassed in a more generalized assemblage sometimes recognized as the Carolinian province (Hedgpeth, 1953). Primarily Antillean in its affinities, the Carolinian province is distinct from the Virginian province to the north and this fact has been emphasized by numerous authors.

Bathymetric limits included in this revised handbook are altered somewhat from the original. Species which occur from the heads of estuaries to the 100-fathom contour are included. Freshwater decapods, included in the original, have been excluded because they never occur in the marine environment. Species that occur only beyond the 100-fathom line more properly belong to a deep-sea fauna that ranges far beyond the Carolinian province, and are not included.

Arbitrary limits are difficult to establish. Judgments undoubtedly will differ as to what is extralimital and what is not. For some species with uncertain distributional limits, a list of extralimital species has been included.

An analysis of the decapod crustacean element in the Carolinian fauna is given by family in table 1. Here, categories chosen for limits in geographic range are used broadly, especially at their southern extremities. For economy of space, the term "South America" can mean either the northern or southern Atlantic shores of the continent, but details are given in the species accounts. Our interest here centers primarily on the eastern coast of North America, and on natural boundaries or barriers that exist on this stretch of coast.

It is apparent that a small number (6.8 percent) of Carolinian decapods are northern in affinity, extending to southern Florida in one case (*Cancer borealis*). To this group, Cape Cod is no barrier, but to another group (12.7 percent) it is a barrier to northward extension into upper New England and the Maritime Provinces of Canada.

Totals are given for species extending northward to the Middle Atlantic States (9.1 percent). Many of these records are for accidental or seasonal occurrence; *i.e.*, species whose northern limits of range might well be set at Cape Hatteras. But there are other species in the group which must be permanent residents in those latitudes and are not dependent on annual repopulation from breeding stock to the south.

Cape Hatteras is a barrier to northward distribution of shallow-water forms. Here, warm water of the Gulf Stream meets the cold Labrador Current to be deflected seaward (Hutchins, 1947), and 27.7 percent of the decapods are apparently unable to bridge the narrow transition zone to colder water.

Cape Lookout, surprisingly, seems to be a greater barrier to northward extension of range among Antillean species (31.4 percent) than Cape Hatteras. This barrier may be real, or it may be that faunal limits fluctuate between these capes as a consequence of natural events. More likely is the fact that far more collecting has been done near Cape Lookout than at Cape Hatteras because of the nearness of marine laboratories to the former.

Species showing distributions reaching northward only to Charleston, S.C., (4.5 percent) are probably southern species with accidental records at that latitude, for there is no apparent barrier to dispersal in that area. Eastern and western Atlantic forms are equally small in number (4.5 percent).

Cosmopolitan species (1.8 percent) are few, as are endemic species (1.4 percent).

Aside from the above patterns of distribution, a number of species ranging along the Atlantic coast and the Gulf coast to Texas have a disjunct distribution in peninsular Florida. The number of these species is conservatively estimated, from literature records, at 10 percent of the total. This type of distribution, discussed at length by Hedgpeth (1953), shows a fairly recent separation of Gulf elements from the Atlantic portion of the species by emergence of peninsular Florida, but with the two areas being climatically equivalent

FIGURE 1.—Area of western North Atlantic Ocean, including portions of eastern North America, Middle America, and northern South America, covering centers of distribution for most species treated in this handbook.

(Hutchins, 1947). It is also clear, from families represented in this group, that many are relatively sedentary, at least as adults.

MATERIALS STUDIED

Materials studied at the U.S. National Museum (USNM) include recent records resulting from exploratory work by the vessels *Pelican*, *Albatross III*, *Combat*, *Oregon*, and *Silver Bay*, as well as records of collections by private individuals. Specimens studied were from the USNM, the Charleston Museum, Charleston, and Bears Bluff Laboratories, Wadmalaw Island, S.C., The University of North Carolina Institute of Fisheries Research (IFR), and various collections provided by Duke University Marine Laboratory and the U.S. Fish and Wildlife Service, Bureau of Commercial Fisheries Biological Laboratory, Beaufort, N.C. Remnants of Hay and Shore's collections were also examined and are now housed at the IFR.

MEASUREMENTS

Measurements for individuals considered adult are either from the literature or from specimens examined. Sizes recorded usually represent the maximum. Width of the brachyuran carapace is the width including lateral spines. Length of shrimps includes the rostrum.

EXTRALIMITAL AND INDETERMINATE SPECIES

The following list includes species having doubtful position in the Carolinian fauna. Some range primarily in deep water, occurring incidentally on the Continental Shelf. Others have a range limited to shallow waters distant from the Carolinas. Some are included because Hay and Shore mentioned them, and the remainder have a doubtful taxonomic status.

Penaeopsis megalops (Smith). North Carolina, through Gulf of Mexico to Surinam; 150–200+ fathoms.

Sicyonia sp. (Lunz, 1945). A distinct specimen from Beaufort River, near Parris Island, S.C., has been described but not named (Charleston Museum No. 35.131.5(a)).

Hippolyte coerulescens (Fabr.). Central Atlantic Ocean, Bermuda, North Carolina to Florida, Azores, Canary and Cape Verde Islands, Gulf of Guinea and S. Angola, doubtful from Cape Horn region (Sivertsen and Holthuis, 1956). A single mutilated male from Sneads Ferry, N.C., is in the U.S. National Museum.

Homarus americanus H. Milne Edwards. Labrador to North Carolina; shallow water to 100+ fathoms. The American lobster is not normally found south of Cape Hatteras, but lobsters are frequently taken off Cape Henry, Va. For instance, one 5½-lb. and two 8–10-lb. lobsters were taken by the trawler *Ensign* approximately 45 miles E.N.E. Oregon Inlet, N.C., at 38–45 fathoms, January 21, 1963. In December 1958, an American lobster was caught in a crab pot near Cedar Island, N.C. Mr. Clayton Fulcher, Atlantic, N.C., reported that he tried to get the specimen, but this prize was eaten by the fisherman's family. Hay and Shore (1918) cited one doubtful occurrence of the lobster near Beaufort, N.C.

Munida longipes H. Milne Edwards. South Carolina to Curaçao; 154–338 fathoms (Schmitt, 1935a).

Pagurus cokeri Hay. South of Cape Lookout, N.C., to eastern Gulf of Mexico; approximately 150–200 fathoms.

Catapagurus sharreri Milne Edwards. Between Capes Hatteras and Lookout, N.C., to Barbados; 87–221 fathoms.

Latreillia elegans Roux. Both sides of North Atlantic Ocean, Mediterranean Sea, Natal; 70–200 fathoms (Rathbun, 1937).

Portunus ventralis (Milne Edwards). Georgia or Florida to Brazil; surface and near shore (Rathbun, 1930a).

Portunus sebae (Milne Edwards). Hay and Shore (1918) cited reports of this species in the Carolinas. Gulf of Mexico and Florida Straits to Brazil, Bermuda; surface to 15 fathoms.

Callinectes danae Smith. Status of this species on the southeastern coast of the United States needs clarification for there is no clear distinction there between it and *C. ornatus*. Indian River Inlet, Fla. to Brazil; shallow water to a few fathoms.

Parapinnixa hendersoni Rathbun. This species is questionably recorded from lat. 34°34′ N. long. 75°50′ W., southeast of Cape Lookout, N.C., 35

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TABLE 1.—*Geographic ranges of decapod crustaceans*

[Lower portion of table shows combined totals of species with ranges limited by natural

Families	Number of species	North of Cape Cod to Florida, Gulf of Mexico, West Indies and South America	Cape Cod to east Gulf of Mexico and West Indies	Cape Cod to west Gulf of Mexico and South America	Middle Atlantic States to west Gulf and Caribbean	Middle Atlantic States to South America	Hatteras to east Gulf of Mexico, West Indies, and South America	Hatteras through Gulf of Mexico and West Indies to South America	Hatteras to west Gulf of Mexico
Penaeidae	17				1	3	2	4	2
Pasiphaeidae	1						1		
Palaemonidae	14	1		2		1	1	1	1
Gnathophyllidae	1								
Alpheidae	10	1						5	
Ogyrididae	2				2				
Hippolytidae	8			2	1	1			
Processidae	1								
Pandalidae	1								
Crangonidae	1	1							
Palinuridae	1							1	
Scyllaridae	4							1	
Galatheidae	2								1
Porcellanidae	8			2	1			3	
Callianassidae	3	1							
Paguridae	21	1	1	1		1	5		1
Albuneidae	3								1
Hippidae	2			1					
Raninidae	1								
Dromiidae	3							1	1
Homolidae	1								
Leucosiidae	6				1		1		
Calappidae	9			1	1		1	3	
Portunidae	13	2		3		2		3	
Cancridae	2	2							
Xanthidae	24	3		2	1		3	6	
Goneplacidae	3							1	
Pinnotheridae	10	1	2	3	1				
Palicidae	2							1	1
Grapsidae	6	1		1	1				
Ocypodidae	4	1		3					
Majidae	30		3		1		5	2	
Parthenopidae	6			1		1	2		
Total	220	15	6	22	11	9	21	32	8
		North Cape Cod-South	Cape Cod-South		Middle Atlantic-South		Hatteras-South		
Combined total		15	28		20		61		
Percent total	99. 9	6. 8	12. 7		9. 1		27. 7		

fathoms (U.S. National Museum). Cuba, Gulf of Mexico; 30–35 fathoms.

Parapinnixa beaufortensis Rathbun. The only specimen of this species known is the holotype from fishing grounds, 20 miles off Beaufort Inlet, N.C. Rathbun (1918b) doubtfully referred this form to the genus *Parapinnixa* and believed that it was a postlarval stage of an unknown species because of small size, relatively large eyes, hairiness of legs and carapace, and thin gripping edges of the fingers suggesting that in another molt or two gaping fingers might emerge. I believe that it may be a young *Palicus*.

Notolopas lamellatus Stimpson. Rathbun (1930a) gave one occurrence of an ovigerous female off Beaufort, N.C. Sonora, Mexico, to Ecuador (Garth, 1958).

A large amount of unidentified material is in existing collections and some of this contains undescribed species. It is expected that the increase in oceanographic research in Southeastern United States will soon add to knowledge of decapod crustaceans in the area.

GLOSSARY

Many of the structures listed alphabetically and defined are shown schematically on figures

barriers. Numbers marked with an asterisk duplicate numbers in adjacent columns]

Eastern and western Atlantic	Pacific	Cosmopolitan	Endemic	Disjunct at Florida Peninsula	Lookout to east Gulf of Mexico and West Indies	Lookout to east Gulf of Mexico, West Indies, and South America	Lookout through Gulf of Mexico, West Indies, and South America	Charleston to West Indies, Texas or South America
1+*1	*1	1		*1	1	1	1	
				0				
1	*1	2		*4	2	1	1	
			1	0				
	*2			0	1	1	2	
				*1				
2				0			1	1
			1 (restr.)	0				
				0	1			
	*1			0				
				0				
				0	1	2		
				0			1	
	*1			0	1			1
				*2		1	1	
				*4	2	5	2	2
1				*1			1	
				*2				1
				0	1			
				0		1		
1				0				
				0	3	1		
				0	2			1
1				0	1			1
				0				
				0	2	1	6	
				0			2	
			1	*5	1		1	
				*1				
2	*1	1		*2				
1				0	4	6	5	3
				0		2		
10+*1	*7	4	3	*23	23	22	24	10
East and west Atlantic		Cosmopolitan	Endemic		Lookout–South			Charleston–South
10+*1		4	3		69			10
4. 5		1. 8	1. 4	*10. 5	31. 4			4. 5

2, 3, and 4. Other terms not listed are shown on these figures.

Acicle.—Antennal scale which is reduced to a spine.

Afferent channels.—Openings through which water passes to the gills. In brachyuran crabs, usually opening behind the pterygostomian regions and in front of chelipeds except in certain Oxystomata in which they open at anterolateral angles of palate or endostome.

Antennal spine.—Spine on anterior edge of carapace immediately below orbit adjacent to base of antenna (fig. 2).

Anterolateral teeth.—Teeth on anterolateral border of crabs between orbit and lateral spine, exclusive of outer orbital teeth.

Apodeme.—Any cuticular ingrowth of body wall.

Appendix interna.—Small separate branch on medial side of pleopodal endopodite tipped with hooks which interlock with opposite member in swimming.

Appendix masculina.—Accessory male organ located medially on second pair of pleopods between endopodite and appendix interna.

Arthrobranchiae.—Gills attached to articular

membrane between the coxa of an appendage and the body wall.

Basis (*basipodite*).—Second article (from the body) of a leg or maxilliped. Sixth segment from distal end of the limb.

Basicerite.—Spine on dorsal side of basis of antenna; sometimes more lateral than dorsal.

Branchiocardiac groove.—Groove separating branchial and cardiac regions.

Branchiostegal spine.—Spine on anterior edge of carapace, or near it, immediately below branchiostegal groove (fig. 2).

Branchiostegite.—Part of carapace not coalesced ventrally with the thoracic somites, but overhanging on each side as a covering for chamber in which the gills are concealed.

Buccal cavity.—Cavity on ventral surface of body in which the mouthparts are situated; it is bounded anteriorly by the epistome, laterally by the free edges of the carapace.

Carina.—A keellike ridge or prominence.

Carpus (*carpopodite*).—Third article from the distal end of a leg.

Cervical groove.—Complex groove or series of grooves running across carapace. It is transverse at the middle, then turns obliquely forward (and outward in brachyurans) to the anterolateral margin.

Chela.—Arrangement of the distal two articles of a crustacean limb by which the terminal element is opposed to the element which precedes it, so that the appendage is adapted for grasping.

In a true chela, the elements are shaped as fingers which close against each other.

In a subchela, the terminal article (dactyl) usually closes against the distal surface of the penultimate article (propodus).

Chelipeds.—Pair or pairs of thoracic legs immediately behind the maxillipeds. They bear chelae, or pincer claws, and are often stouter, sometimes much stouter, than the succeeding walking legs.

Coxa (*coxopodite*).—First or proximal article of a leg or maxilliped.

Dactyl (*dactylus* or *dactylopodite*).—Terminal or distal article of a leg or maxilliped. The dactyl is the movable finger of a cheliped.

Efferent channels.—Channels through which water passes from the gills. These open at the sides of the endostome, except in the superfamily Oxystomata in which they open at the middle of the endostome.

Endognath.—Inner or principal branch of a maxilliped.

Endopodite.—Medial ramus of a biramous appendage.

Endostome.—Part of the epistome which forms the palate in brachyurans and is usually separated from the epistome proper by a transverse ridge.

Epibranchial (*epibranchial region*).—Portion of the porcellanid (crab) carapace which is situated behind the orbit and above the metabranchial region. The region situated between the cervical groove and the *linea anomurica.* There is often a strong spine on the region, referred to as the epibranchial spine.

Epigastric lobes.—Anterior lobes or subregions of the gastric region.

Epimere.—A lateral part of the wall of body somites situated between the tergum and the insertion of appendages.

Epipodite.—Outgrowth of the first seven thoracic coxae.

Epistome.—The antennal sternum is mainly represented by the epistome, a plate of varying shape, lying between the labrum and the bases of the antennae. In Natantia the epistome is compartively narrow, and on each side is separated from the lateral portions of the carapace by the exhalant branchial channels. In most of the Reptantia, the epistome is broad and comes in contact with the carapace on each side; in the Brachyura, it becomes firmly united with the carapace. In this way, there is defined, more or less distinctly, a buccal frame within which lie the mouth parts, and which in most Brachyura is closed by the operculiform third maxillipeds. The sides of this buccal frame are formed by the free anterolateral margins of the carapace.

Exognath.—Outer or secondary branch of a maxilliped.

Exopodite. Lateral ramus of a biramous appendage.

Fingers (*digits*).—Narrow scissorlike blades of the claw end of a cheliped, with the movable finger being the dactyl, and the immovable finger the terminal part of the propodus.

Front. Frontal portion of carapace; that portion of the carapace of a crab which lies between the orbits.

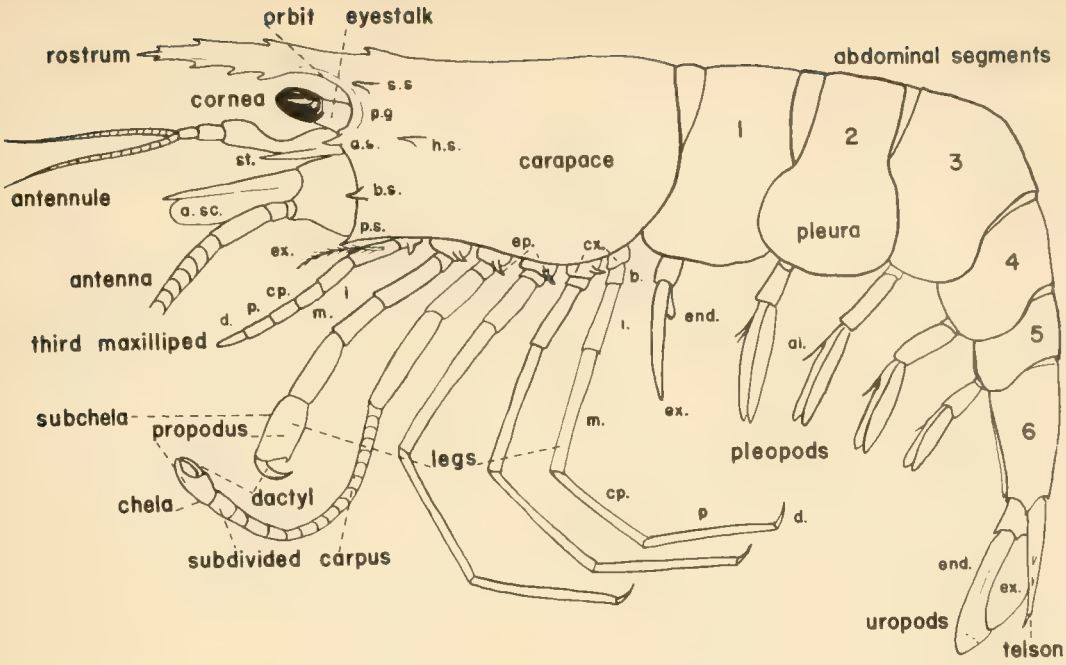

FIGURE 2.—Schematic drawing of shrimp in lateral view; ai., appendix interna; a.s., antennal spine; a. sc., antennal scale; b., basis; b.s., branchiostegal spine; cp., carpus; cx., coxa; d., dactyl; end., endopod; ep., epipod; ex., exopod; h.s., hepatic spine; i., ischium; m., merus; p., propodus; p.g., postorbital groove; p.s., pterygostomian spine; s.s., supraorbital spine; st., stylocerite. (Modified after Holthuis, 1955; Schmitt, 1921.)

Frontal teeth.—True frontal teeth; those teeth originating on the front but exclusive of the inner orbital teeth.

Gastric region.—Large median area, in the crab carapace, bounded behind by the cervical suture, laterally by the hepatic regions, and anteriorly by the frontoorbital regions. It is divisible into the following subregions or lobes: epigastric, protogastric, mesogastric, metagastric, and urogastric.

Genital region.—See urogastric lobe.

Hand (*chela*).—Propodus and dactyl of the cheliped.

Hepatic region.—A small (paired) subtriangular, anterolateral region, wedged between branchial and gastric regions, and either margin of carapace or margin of orbit in Brachyura.

Hepatic spine.—Spine on hepatic region in Natania (fig. 2).

Ischium (*ischiopodite*).—Fifth article of a leg or maxilliped from the distal end. It is usually the first large article of the maxilliped.

Merus (*meropodite*).—Fourth article from the distal end of a leg or maxilliped. It is sometimes called the arm of a cheliped.

Mesogastric lobe.—Lobe or subregion which is the median division of the gastric region, pentagonal in form, and with a long, narrow, anterior prolongation.

Metabranchial (*metabranchial region*).—That region of the porcellanid (crab) carapace which is situated below the *linea anomurica* and, therefore, not completely united with the main portion of the carapace.

Metagastric lobe.—Posterolateral lobe or subregion of the gastric region; often not defined.

Ocellus.—Little eye, distinct from the main organ of vision.

Orbit.—Cavity in the carapace containing the eye.

Orbital region.—Narrow space bordering upper margin of orbit; not always distinguishable.

Palate.—Roof of buccal cavity in crabs.

Palm.—Proximal portion of propodus of chela.

Petasma.—Endopodite of the first pleopods in male Penaeidae. It takes the form of a complicated membranous plate bearing coupling hooks medially which interlock with the member of the

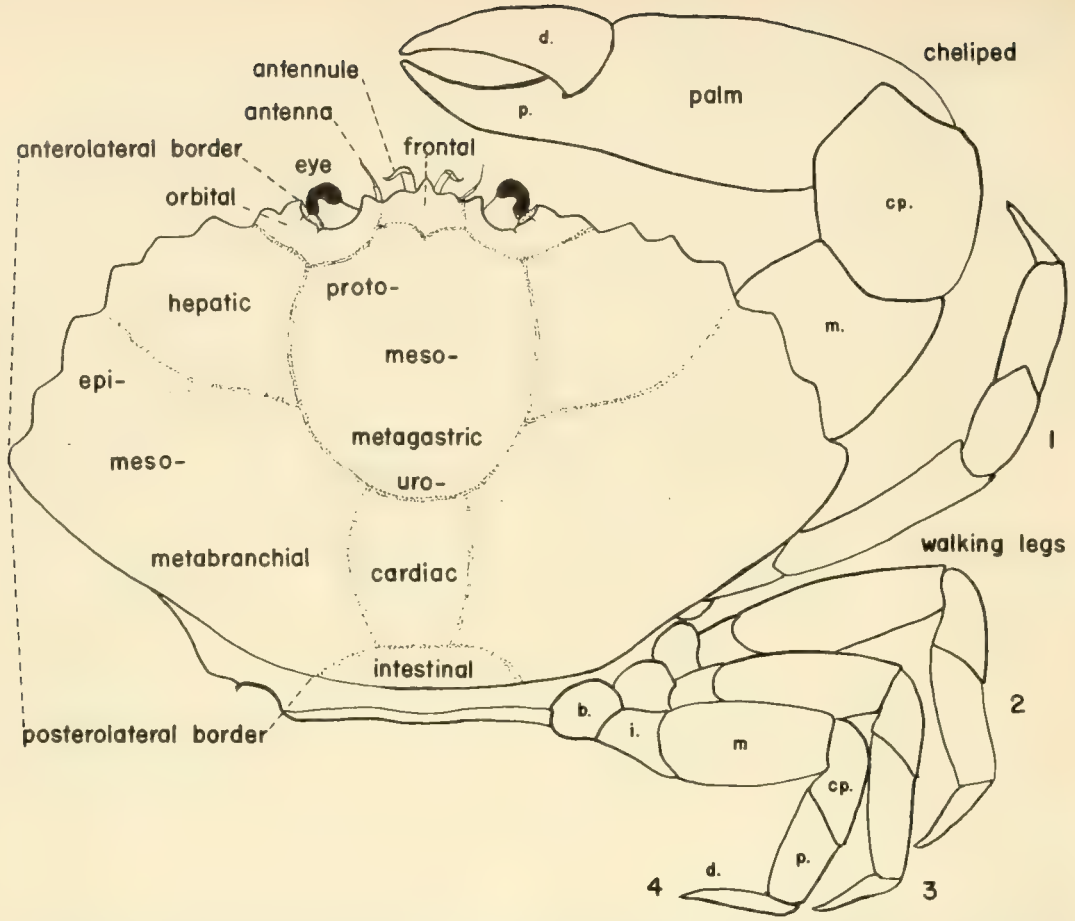

FIGURE 3.—Schematic drawing of brachyuran crab in dorsal view; areas of carapace indicated; legs of right side only shown; b., basis; cp., carpus; d., dactyl; i., ischium; m., merus; p., propodus.

opposite side. The petasma may terminate distally in various combinations of complex-shaped lobes. According to position, these have been termed: distolateral, distoventral, and distomedian. Additional complex processes may also be present.

Pleurobranchia.—Gills attached to lateral wall of body dorsal to the articulation of an appendage.

Podobranchia.—Gills attached to the coxa of an appendage.

Postorbital groove.—Groove on carapace behind orbit and more or less parallel to margin of orbit (fig. 2).

Propodus (*protopodite*).—Second article from the distal end of a leg or maxilliped. In a cheliped, the propodus consists of a palmar portion and a narrower, immovable finger.

Prosartema (*dorsal eye brush*).—Long, thin, ciliated lobe arising dorsally from proximomedial border of first antennular segment and extending anteriorly; found in family Penaeidae.

Protogastric lobe.—Lobes or subregions which are the anterolateral lobes of the gastric region.

Protopodite.—Peduncle of an appendage; in unmodified form, it consists of one coxal and one basal article.

Pterygostomian region.—Triangular space on ventral surface of carapace, on either side of buccal cavity in Brachyura. Region at anterolateral corner of carapace in Natantia.

Pterygostomian spine.—Spine at anterolateral (anteroventral) corner or border of carapace (fig. 2).

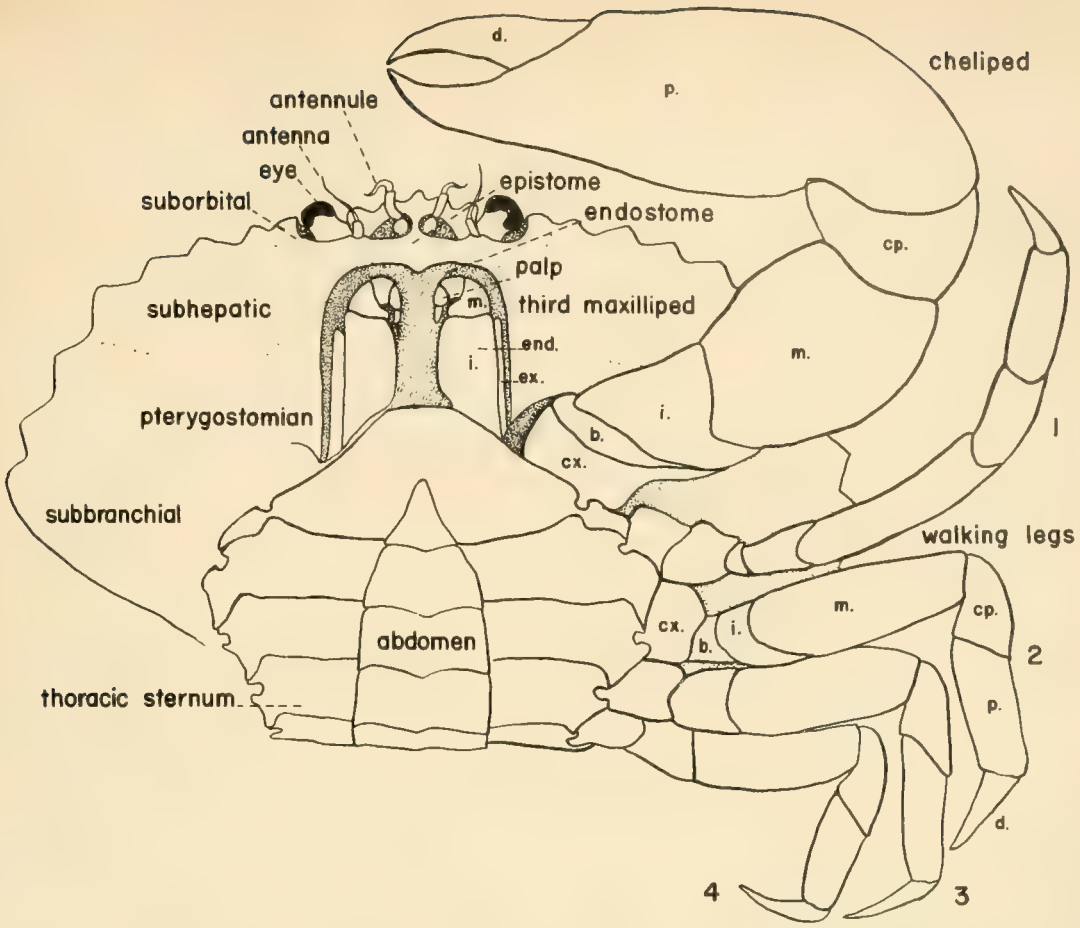

FIGURE 4.—Schematic drawing of brachyuran crab in ventral view; areas of carapace indicated; legs of left side only shown; b., basis; cp., carpus; cx., coxa; d., dactyl; end., endognath; ex., exognath; i., ischium; m., merus; p., propodus.

Scaphocerite.—Antennal scale (fig. 2).

Stylocerite.—Spine or rounded lobe on lateral aspect of basal article of antennules.

Subhepatic region.—Area below the hepatic region and below the anterolateral border of the carapace.

Suborbital spine.—Spine on lower rim of orbit (fig. 2).

Supraorbital spine.—Spine above and behind orbit (fig. 2).

Telson.—Terminal somite of the abdomen except in the Brachyura.

Tergite.—Dorsal plate of a segment.

Thelycum.—External seminal receptacle, variously developed, lying on sternum of the thorax and formed by outgrowths from the last and next to last thoracic somites.

Urogastric lobe.—Posteromedian lobe or subregion of the gastric region; sometimes called the genital region.

ORDER DECAPODA

Caridoid facies either retained or greatly modified. Exopodite of maxilla (scaphognathite or bailer) large. First three pairs of thoracic limbs specialized as maxillipeds. Gills typically in several series, attached to coxae of thoracic limbs, to their articular membranes, and to lateral walls of thoracic somites (podo-, arthro-, and pleurobranchia); rarely absent. Young rarely hatched in nauplius stage (Calman, 1909).

KEY TO SUBORDERS, SECTIONS, SUPERFAMILIES, AND FAMILIES OF DECAPOD CRUSTACEANS FOUND IN THE CAROLINAS

a. General form shrimplike; abdomen well developed and usually with carapace compressed; pleopods always present in full number and used for swimming ..... Suborder Natantia (p. 14).
b. Pleura of second abdominal segment not overlapping those of first segment ..... Section Penaeidea (p. 14).
c. First three pairs of legs chelate, all five pairs of legs well developed ..... Family Penaeidae (p. 14).
cc. First three pairs of legs chelate, last two pairs of legs small or wanting ..... Family Sergestidae (p. 38).
bb. Pleura of second abdominal segment overlapping those of first segment ..... Section Caridea (p. 41).
c. First pair of legs chelate or simple.
d. Fingers of chelae on first and second legs slender, cutting edges all pectinate ..... Family Pasiphaeidae (p. 41).
dd. Fingers of chelae on first and second legs variable in thickness; cutting edges of fingers of chelae not all pectinate.
e. Carpus of second pair of legs entire; first pair of legs always with well-developed chelae.
f. Third pairs of maxillipeds pediform; body slender in most species ..... Family Palaemonidae (p. 42).
ff. Third pair of maxillipeds broad, leaflike; body short and thick ..... Family Gnathophyllidae (p. 61).
ee. Carpus of second pair of legs usually subdivided into two or more joints; first pair of legs often asymmetrically chelate.
f. Chelae of first pair of legs distinct, at least on one side.
g. Each of first legs chelate.
h. Eyestalks short, usually covered by carapace; first pair of legs stronger than second ..... Family Alpheidae (p. 62).
hh. Eyestalks medium length or long, not covered by carapace; first pair of legs not stronger than second pair.
i. Rostrum small or wanting; eyestalks long, slender; first two pairs of legs subequal ..... Family Ogyrididae (p. 74).
ii. Rostrum well developed; eyestalks not abnormally lengthened; second pair of legs usually longer or stronger than first ..... Family Hippolytidae (p. 76).
gg. Only one of first pair of legs chelate, opposite leg ending in a simple clawlike dactyl ..... Family Processidae (p. 86).
ff. Chelae of first pair of legs microscopically small or absent ..... Family Pandalidae (p. 87).
cc. First pair of legs subchelate ..... Family Crangonidae (p. 88).
aa. General form lobsterlike or crablike; abdomen either well developed or greatly reduced in size, usually with abdomen and carapace depressed; pleopods reduced or absent, not used for swimming ..... Suborder Reptantia (p. 90).
b. Abdomen extended, symmetrical, with well-developed tail fan ..... Section Macrura (p. 90).
c. Abdomen well armed, pleura well developed; third pair of legs like first ..... Superfamily Scyllaridea (p. 90).
d. Body subcylindrical; antennae with strongly developed flagella ..... Family Palinuridae (p. 91).
dd. Body strongly depressed; antennae short, squamiform ..... Family Scyllaridae (p. 94).
cc. Abdomen more or less membranous; pleura small or wanting; third legs unlike first, never chelate ..... Superfamily Thalassinidea; Family Callianassidae (p. 99).
bb. Abdomen bent upon itself or flexed beneath thorax; pleura usually small or wanting; tail fan variable in development; (third pair of legs unlike first, never chelate).
c. Uropods usually present, often reduced in size, sometimes united with telson; last thoracic sternite free; carapace not apparently fused with epistome ..... Section Anomura (p. 104).
d. Abdomen well developed.
e. Abdomen symmetrical, more or less flexed beneath thorax; body depressed; tail fan well developed ..... Superfamily Galatheidea (p. 104).
f. Form somewhat lobsterlike; rostrum well developed ..... Family Galatheidae (p. 104).
ff. Form crablike (*Euceramus* elongate); rostrum short and broad or wanting ..... Family Porcellanidae (p. 106).
ee. Abdomen asymmetrical; tail fan reduced and adapted for holding body in hollow objects ..... Superfamily Paguridea; Family Paguridae (p. 114).
dd. Abdomen much reduced in size and flexed under thorax ..... Superfamily Hippidea (p. 136).
e. First pair of legs subchelate; carapace depressed ..... Family Albuneidae (p. 136).
ee. First pair of legs simple; carapace subcylindrical ..... Family Hippidae (p. 139).

aa. General form lobsterlike or crablike—Continued
bb. Abdomen bent upon itself or flexed beneath thorax—Continued
cc. Uropods rarely present, never biramous; abdomen small, permanently flexed beneath thorax; carapace fused with epistome; (first pair of legs always chelate or subchelate) ..... Section Brachyura (p. 142).
d. Anterior thoracic sterna very broad, posterior thoracic sterna narrow and keellike; posterior thoracic epimera largely exposed by reduction of branchiostegite ..... Subsection Gymnopleura; Family Raninidae (p. 142).
dd. Anterior thoracic sterna not usually broad, posterior thoracic sterna not keellike; posterior thoracic epimera covered by branchiostegite.
e. Buccal frame triangular, prolonged forward to form a gutter; openings of oviducts generally sternal; first pleopods lacking in female ..... Subsection Oxystomata (p. 146).
f. Afferent branchial openings on either side of endostome ..... Family Leucosiidae (p. 147).
ff. Afferent branchial openings in front of bases of chelipeds ..... Family Calappidae (p. 152).
ee. Buccal frame roughly quadrate; not prolonged forward.
f. Last pair of legs modified in form and dorsal in position; openings of oviducts coxal; first pleopods present in female ..... Subsection Dromiacea (p. 143).
g. Sternum of female with longitudinal grooves; eyes usually completely sheltered by orbits when retracted ..... Family Dromiidae (p. 143).
gg. Sternum of female without longitudinal grooves; eyes incompletely or not at all sheltered by orbits when retracted ..... Family Homolidae (p. 146).
ff. Last pair of legs normal in position (rarely reduced or dorsal, Palicidae); openings of oviducts on sternum; first pleopods lacking in female ..... Subsection Brachygnatha (p. 160).
g. Body of medium width or broad in front; rostrum reduced or wanting. ..... Superfamily Brachyrhyncha (p. 160).
h. Carpus of third maxillipeds articulating at or near anterointernal angle of merus; body usually round or transversely oval; openings of vasa deferentia nearly always coxal.
i. Distal articles of last pair of legs broad, thin and paddlelike ..... Family Portunidae (p. 160).
ii. Distal articles of last pair of legs not paddlelike.
j. Antennules folding longitudinally; outer maxillipeds long, overlapping epistome ..... Family Cancridae (p. 174).
jj. Antennules folding transversely or obliquely; outer maxillipeds usually not overlapping epistome.
k. Body usually transversely oval; openings of vasa deferentia rarely sternal ..... Family Xanthidae (p. 176).
kk. Body usually quadrate; openings of vasa deferentia sternal or, if coxal, passing along groove in sternum ..... Family Goneplacidae (p. 201).
hh. Carpus of third maxillipeds not articulating at or near inner angle of merus; body usually quadrate (except Pinnotheridae); openings of vasa deferentia nearly always sternal; right chela not always larger than left (except Palicidae).
i. Small, usually commensal crabs with small eyes and orbits; body usually somewhat rounded, adult females often with carapace somewhat membranous ..... Family Pinnotheridae (p. 203).
ii. Free living crabs with eyes not strikingly reduced; body usually quadrate, adult females with carapace normal.
j. Last pair of legs dorsally placed and weaker than others; interantennular septum very thin ..... Family Palicidae (p. 215).
jj. Last pair of legs not dorsally placed; not markedly weaker than others; interantennular septum not very thin.
k. Front broad; eyestalks of moderate length or short; a gap of varying size between outer maxillipeds ..... Family Grapsidae (p. 217).
kk. Front with moderate width; eyestalks long; outer maxillipeds nearly, or quite, closing buccal area ..... Family Ocypodidae (p. 225).
gg. Body narrowed in front; rostrum usually distinct; orbits often incomplete ..... Superfamily Oxyrhyncha (p. 235).
h. Chelipeds not much larger than other legs ..... Family Majidae (p. 236).
hh. Chelipeds much larger than other legs ..... Family Parthenopidae (p. 266).

Systematic and Ecological Discussion

Suborder **Natantia**

Body almost always laterally compressed. Rostrum usually compressed and serrated. First abdominal segment not much smaller than rest. Antennules generally with stylocerite; antennal scale generally large and lamellar. Legs usually slender, except sometimes a stout chelate limb or pair, which may be any one of first three pairs; with basipodite and ischiopodite very rarely coalesced and with only one fixed point in carpopropodal articulation (with some doubtful exceptions); sometimes with exopodites; podobranchiae hardly ever present on first three and never on last two pairs; male genital apertures in articular membrane. Pleopods always present in full number, well developed, used for swimming (Calman, 1909).

Section **Penaeidea**

Pleura of second abdominal segment not overlapping those of first segment. Antennules generally with stylocerite. Mandibular palps straight. First maxillipeds without expansion at base of exopodite, endopodite long; second maxillipeds with terminal articles normal; third maxillipeds with seven articles. Third legs chelate (except when much reduced), not stouter than first pair. First pleopods of male bearing sexual apparatus (Calman, 1909).

Family **Penaeidae**

Body somewhat or considerably compressed. Rostrum usually well developed, laterally compressed, often with teeth. Eyes moderate or greatly elongate. Antennules with two flagella; basal article of peduncle hollowed out dorsally for eye, with stylocerite on basal outer margin. Mandible with incisor process and palp of one or two articles. First three pairs of legs similar, chelate, slender, increasing in length posteriorly; fourth and fifth legs well developed, simple (Schmitt, 1921).

Remarks.—For most species treated in this handbook information on natural history is included in the separate species accounts. In the case of parasites found in certain penaeids, such citation has proved too cumbersome. Parasites in this group have been studied only recently. Host specificity and life cycles of the parasites are imperfectly known and identification of some forms is uncertain. The interested student is referred to a review of most of the known parasites given by Hutton, Sogandares-Bernal, Eldred, Ingle, and Woodburn (1959), and Iversen and Manning (1959).

Spelling of the name *Penaeus* and related generic names has unfortunately not been uniform. Gunter (1957) reviewed these circumstances and re-emphasized that under the International Code, original spelling must be observed. He included a list of the genera of Penaeidae.

KEY TO SUBFAMILIES IN THE CAROLINAS

a. Postorbital spine present_____Solenocerinae (p. 14).
aa. Postorbital spine absent.
  b. Carapace without a median dentate crest, except occasionally over eyes_____Penaeinae (p. 17).
  bb. Carapace with a median dentate crest extending nearly or entirely to posterior margin
Sicyoninae (p. 32).

Subfamily **Solenocerinae**

Carapace with postorbital spine, cervical groove extending nearly or quite to dorsum. Ocular peduncle with a distinct tubercle, a scale at external angle of ocular somite. Antennular peduncle with an enlarged ciliated protuberance on inner proximal margin of basal article. First chelipeds with tuft of setae on propodus in both sexes. Coxae from second maxillipeds to fifth legs with weakly forked epipodites. A functional filamentose anterior arthrobranch on 13th somite (4th leg); pleurobranchs behind 9th somite (3d maxilliped). Exopodites on maxillipeds and legs. Pleopods, except first pair, biramous. Telson with well-developed terminal point and a pair of subterminal fixed spines (Burkenroad, 1934b).

KEY TO GENERA AND SPECIES IN THE CAROLINAS

a. Antennular flagella hollowed out medially, channellike in structure_____*Solenocera atlantidis* (p. 15).
aa. Antennular flagella not hollowed out medially nor channellike in structure
Hymenopenaeus tropicalis (p. 15).

Genus *Solenocera* Lucas, 1849

Burkenroad, 1934b, p. 64.—1936, p. 120.—1939, p. 6.

Solenocera atlantidis Burkenroad

Figure 5

Solenocera atlantidis Burkenroad, 1939, p. 10.

Recognition characters.—Body compressed, carapace deeper than broad; integument thin, smooth; sides of rostrum and area near base of rostrum covered with short hairs; carapace with small pterygostomian spine meeting frontal margin at right angle, spine sometimes doubled; postorbital and hepatic spines well developed; antennal angle acute, more or less toothlike, often not greatly produced; orbital angle with a distinct spine on margin; cervical groove reaching middorsal line; branchiocardiac groove prominent. Rostrum not reaching distal edge of eye; lower margin unarmed, convex; with five to seven, usually six, dorsal teeth not counting dagger-shaped tip, two behind, one above orbital margin, posterior tooth slightly remote from others. Postrostral carina not continued beyond crossing of cervical groove. Antennular flagella slender, about half as long as body; lower flagellum broader than upper at hollowed basal portion. Antennal scale extending no more than one-tenth its length beyond antennular peduncle.

Coxa of fifth legs with strong tooth on anteromedial margin in both sexes.

Abdomen with last three segments carinate; third to fifth segments cleft posterodorsally at midline; sixth segment with a spine at middorsal posterior and posterolateral corners and a toothlike projection at middle of distolateral edge. Telson short, broad, lateral spines large. Exopods of uropods with no spine at distolateral corner.

Measurements.—Length of body: large male, 37 mm.; large female, 56 mm.

Variations.—The epipodites are usually mitten-shaped, but sometimes more distinctly forked, the thumb or inferior branch never exceeding the proximal or palmar portion of the blade, exclusive of the peduncle.

Color.—Orange red, color most concentrated as bands across posterior parts of abdominal tergites (Burkenroad, 1939).

Habitat.—Mud, shell, and coral bottoms; 10 to 180 fathoms.

Type locality.—Gulf of Mexico off Alabama (*Atlantis* station 2813, roughly lat. 30° N. long. 88° W.), 19 fathoms.

Known range.—Cape Hatteras, N.C., to near Campeche, Mexico; Surinam (Hildebrand, 1955; Holthuis, 1959).

Remarks.—Females with well-ripened ovaries have been taken in March off Alabama (Burkenroad, 1939).

Genus *Hymenopenaeus* Smith, 1882

Burkenroad, 1936, p. 102.

Hymenopenaeus tropicalis (Bouvier)

Figures 6–7

Parartemesia tropicalis Bouvier, 1905, p. 749.
Haliporus tropicalis: Bouvier, 1906, p. 4.—Milne Edwards and Bouvier, 1909, p. 247, pl. 3, figs. 1–9, text-figs. 45–54.
Hymenopenaeus tropicalis: Burkenroad, 1936, p. 102.
Solenocera weymouthi Lindner and Anderson, 1941, p. 181, fig. 1.

Recognition characters.—Body robust, laterally compressed; integument thin, polished, except finely setose at sides of rostrum and area near base of rostrum; carapace deeper than broad with antennal, hepatic, and postorbital spines well developed, a small stout spine on orbital margin; cervical groove extending nearly to middorsal line; branchiocardiac groove extending from near anterolateral corner to level of base of first legs. Rostral crest not extending beyond level of cervical groove, armed above with 7 to 10 teeth excluding rostral tip, posterior tooth slightly remote from others; rostrum reaching about to distal edge of eye, straight or slightly upturned at tip, lower edge convex, unarmed, ciliated. Prosartema prominent, hairy, extending to or beyond middle of second segment of antennular peduncle. Antennular flagella somewhat flattened, upper ramus about one-third diameter of lower at base. Antennal flagella about three times body length.

Female with projections on coxae of last three pairs of legs, first pair posteromedial and blunt pointed; second pair medial, bladelike, with thin, styliform posterior projection; third pair medial, broad, bladelike, partially covering thelycum. Thelycum setose, posterior lateral lobes united; middle lobes rounded, discrete; anterior lobes closely approximated at midline, partially covered by coxal projections of fourth legs.

Abdomen with middorsal carina low and faint on third segment, progressively more prominent

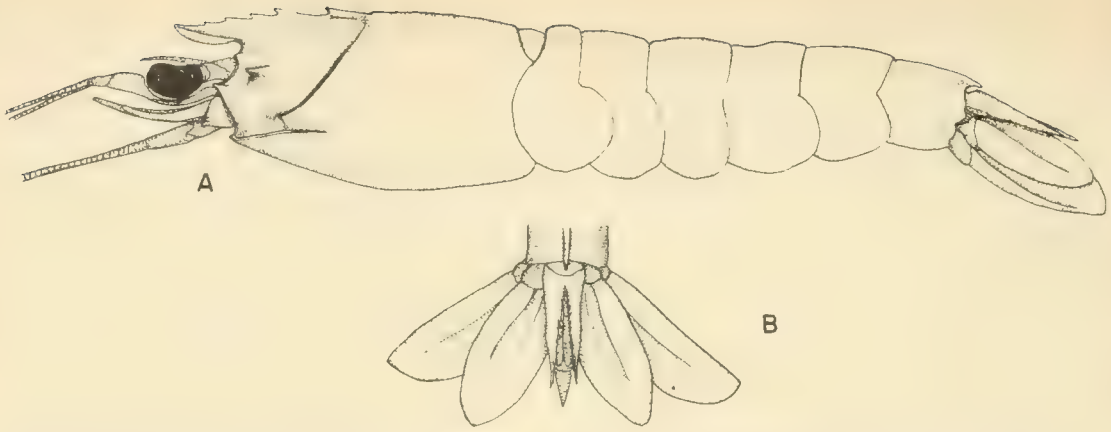

FIGURE 5. *Solenocera atlantidis* Burkenroad. A, animal in lateral view; B, uropods and telson in dorsal view; A–B × 2.5.

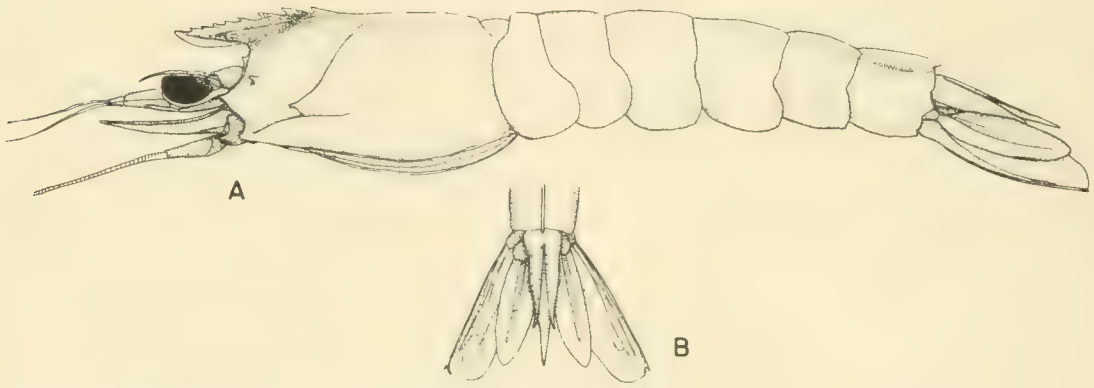

FIGURE 6.—*Hymenopenaeus tropicalis* (Bouvier). A, animal in lateral view; B, uropods and telson in dorsal view; A–B × 1.25.

posteriorly; segments three to five variably cleft posterodorsally; sixth segment with a small middorsal posterior spine, a spine at posterolateral corners, and a toothlike projection at middle of distolateral edge. Telson tapering to a strong point flanked on each side by a strong, fixed, subterminal spine; middorsal groove bifurcated at midlength, forks ending medial to base of fixed spines. Exopods of uropods with small spine at distolateral corner. Male with large, membranous, complexly folded petasma; tips of petasma reaching base of second legs.

Measurements.—Length of body: large male, 56 mm.; large female, 92 mm.

Color.—Red.

Habitat.—Seventeen to 200 fathoms, rarely deeper; usually inside 100-fathom curve.

Type locality.—Florida Bank (Gulf of Mexico), lat. 26°31′ N. long. 85°03′ W.

Known range.—Cape Hatteras, N.C., to Gulf of Mexico, off Alabama.

Remarks.—Burkenroad considered it likely (in Anderson and Lindner, 1945) that *Solenocera*

FIGURE 7. *Hymenopenaeus tropicalis* (Bouvier). Petasma of male in ventral view. 1 mm. indicated.

weymouthi Linder and Anderson was identical with *Hymenopenaeus tropicalis* (Bouvier). Comparison of a number of specimens of both forms leads me to regard them as identical. Prominence of the coxal projections on the last three pairs of legs in females varies with age. Those illustrated by Lindner and Anderson appear not so well developed as in fully matured *H. tropicalis* females.

Subfamily **Penaeinae**

Carapace without postorbital spine; cervical groove not extending to dorsum. Ocular somite without a greatly produced pair of median projections, but with a more or less conspicuous pair of projections from lateral portions; ocular peduncles with some inconspicuous vestiges of a median tubercle. Proximomedian margin of antennular peduncle produced as an elongate scale. First chelipeds with tuft of setae on propodus in both sexes. No podobranchs behind eighth somite (second maxillipeds). No epipodites behind 12th somite (3d legs); epipodites usually forked. No filamentous anterior arthrobranch on 13th somite (4th leg). Pleopods, except first pair, biramous. Telson with well-developed terminal spine (Burkenroad, 1934b).

KEY TO GENERA AND SPECIES (PARTIAL) IN THE CAROLINAS

a. Rostrum with ventral teeth ..... *Penaeus* (p. 17).
aa. Rostrum without ventral teeth.
  b. Telson with subterminal pair of fixed spines.
    c. Carapace with longitudinal and transverse sutures present; body nearly smooth ..... *Parapenaeus longirostris* (p. 27).
    cc. Carapace without longitudinal and transverse sutures; body pubescent ..... *Penaeopsis goodei* (p. 29).
  bb. Telson with no subterminal pair of fixed spines.
    c. Rostrum slender, sinuous, as long as or longer than carapace, with basal thin, high crest armed with five teeth plus an isolated epigastric tooth ..... *Xiphopeneus kroyeri* (p. 30).
    cc. Rostrum not slender and sinuous, about half length of carapace, dorsal teeth evenly spaced ..... *Trachypeneus constrictus* (p. 31).

KEYS TO SPECIES IN THE CAROLINAS

Genus ***Penaeus*** Fabricius, 1798

Burkenrod, 1934b.—Hemming, 1958b.

Adults

(Based on keys by Anderson and Lindner, 1945, and Voss, 1955)

a. Lateral rostral grooves not extending beyond base of rostrum ..... *setiferus* (p. 18).
aa. Lateral rostral grooves reaching almost to posterior margin of carapace.
  b. Petasma of male with external edge of distoventral lobe armed with 2 to 12, usually 4 to 7, spinules; teeth of internal edge of lobe long and sharp in close-set group of 6 to 16. Thelycum of female with anteromedian corners of lateral plates moderately gaping, not covering carina of posteromedian part of median plate on 13th body somite (4th legs) ..... *duorarum* (p. 21).
  bb. Petasma of male with external edge of distoventral lobe smooth, incurved, teeth of internal edge of lobe small, in close-set group. Thelycum of female with anteromedian corners of lateral plates widely gaping, exposing forked carina of posteromedian plate on 13th body somite (4th legs) ..... *aztecus* (p. 24).

JUVENILES BETWEEN 17 AND 47 MM. TOTAL LENGTH, LIVE OR FRESHLY PRESERVED

(Williams, 1953)

a. Lateral rostral grooves not reaching almost to posterior margin of carapace; rostrum prominent and slightly upturned at tip in individuals above 22 mm. total length. Ground color light gray, sometimes with greenish cast in shrimp taken from beds of vegetation; chromatophores (widely spaced except on spines, ridges, and uropods) colored slate-blue and brown; uropods with reddish-brown to brown areas distally ..... *setiferus* (p. 18).
aa. Lateral rostral grooves reaching almost to posterior margin of carapace (shallow in 17 mm. individuals). Color gray to light brown, sometimes with greenish cast in shrimp taken from beds of vegetation; chromatophores numerous and closely spaced, often in bands or patches.
  b. Rostrum usually not upturned at tip. Chromatophores slate-blue and brown; usually with conspicuously pigmented lateral spot at juncture of third and fourth abdominal segments; uropods with uniform sprinkling of chromatophores, degree of transparency uniform throughout (color more dense in older individuals) ..... *duorarum* (p. 21).
  bb. Rostrum usually slightly upturned and attenuate at tip. Chromatophores brown and olive-green; uropods with reddish-brown to brown areas distally ..... *aztecus* (p. 24).

***Penaeus setiferus* (Linn.).** White shrimp

Figures 8–9

? Cancer setiferus Linnaeus [in part]. 1767, p. 1054.
Penaeus setiferus: Hay and Shore, 1918, p. 378, pl. 25, fig. 5.—Burkenroad, 1939, p. 17 (rev.).—Holthuis, 1962, pp. 115–118.
Penaeus fluviatilis: Gunter, 1962a, b, pp. 107–114; 118–121.

Recognition characters.—Integument thin, polished, translucent. Carapace with a high median carina continuous anteriorly with rostrum and extending back about two-thirds length of carapace; not grooved posteriorly, with lateral grooves terminating near posterior tooth in rostral series; armed with 9 or 10 sharp teeth dorsally, anterior 6 teeth on rostrum proper; postocular crest absent. Rostrum with tip long, slender, unarmed, upcurved distally, apex sometimes depressed, first dorsal tooth near distal edge of eye, ventral edge armed with two teeth. Antennal spine surmounting lateral carina extending upward short distance from hepatic spine. Medial antennular flagellum of adult male dorsoventrally flattened and armed dorsally with two sizes of teeth.

Anterolateral marginal ridges of last thoracic sternite of female extending conspicuously mediad near middle of segment making an interrupted crescentic transverse ridge with concavity directed forward; posterior portion of sternite with conspicuous pair of fleshy protuberances. Posterior margin of 12th sternite with pair of posteromedial convexities extending almost level with median portion of margin.

Abdomen with fourth to sixth segments carinate; carina of sixth segment with a groove on each side. Telson with deep median groove and an acuminate tip. Ventral margin of pleura of first abdominal segment almost straight. Petasma of male with diagonal ridge across face of distolateral lobe.

Measurements.—Length of body: large male, 182 mm.; large female, 197 mm.

Color.—Body translucent, bluish white with dusky bands and patches composed of scattered black specks; rostrum and sides tinged with pink; blades of pleopods marked with dark red; antennae dark brown; uropods with tips of blades dark brownish purple with narrow stripe of yellowish green along margin.

Habitat.—Estuaries and inner oceanic littoral, predominantly on mud bottom from water's edge to 17 fathoms off Atlantic coast; rarely to 43 fathoms in Gulf of Mexico (Springer and Bullis, 1952).

Type locality.—Off Matanzas Inlet, Fla.

Known range.—Fire Island, N.Y., to Cape Canaveral, Fla.; Gulf of Mexico from Pensacola, Fla., to Campeche, Mexico; Cuba; Jamaica.

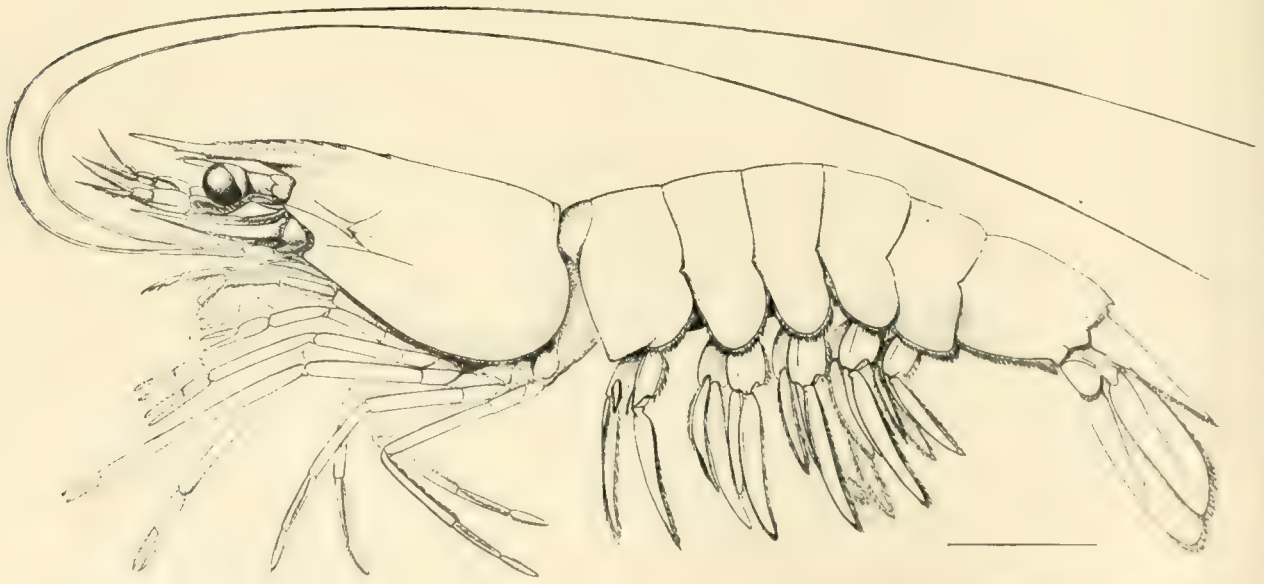

FIGURE 8. *Penaeus setiferus* (Linnaeus). Animal in lateral view; approximately 25 mm. indicated (after Rathbun, 1884).

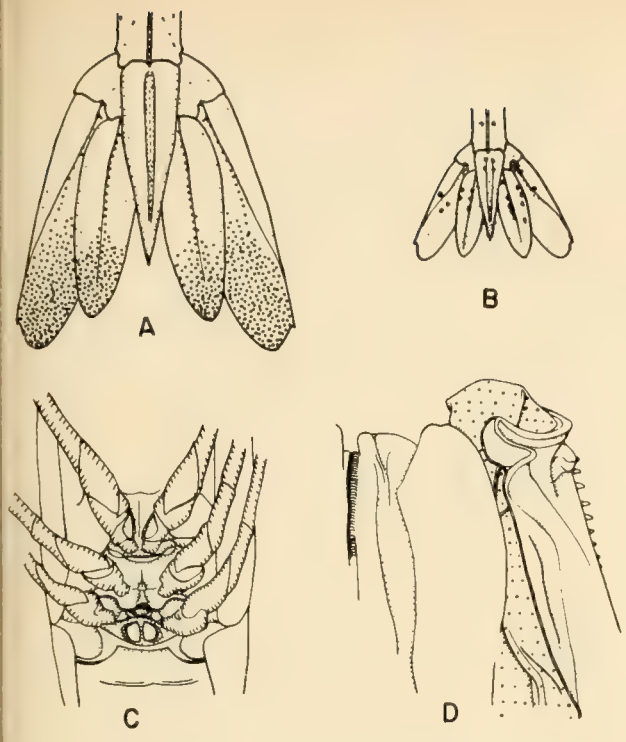

FIGURE 9.—*Penaeus setiferus* (Linnaeus). Chromatophore distribution in tail fan (semidiagrammatic) of A, 17 mm. juvenile, B, 32 mm. juvenile; A–B approximately × 5 (after Williams, 1953). C, thelycum of adult female; D, petasma of adult male, ventral view, distal portion of left half (after Burkenroad, 1934b).

Remarks.—Of the shrimps occurring in the Carolinas, *P. setiferus* has been studied most extensively. This has resulted from the fact that the species has great commercial value, and was the first of the American penaeids to be extensively marketed for food. In the early 1930's, when popular demand caused fishing effort to expand greatly, concern over the possibility of depleting the resource led the U.S. Fish and Wildlife Service to initiate a research program on various aspects of the biology of this species. At that time, *P. setiferus* composed over 95 percent of the commercial catch (Lindner and Anderson, 1956). A voluminous literature, scholarly and popular, has accumulated in the ensuing 30 years, and though it would be presumptuous to attempt a complete review of this work here, the chief results of studies can be outlined. (An exhaustive bibliography has been complied by Chin and Allen, 1959).

Recently (see synonymy) usage of the name *setiferus* for the white shrimp in North America has been questioned. The well-established name *setiferus* would seem best retained here.

The species is caught commercially throughout most of its geographic range (from North Carolina to Mexico); however, by far the greatest concentration occurs in Louisiana, in and near the Mississippi River Delta, and it was here that Viosca (1920) first worked on some aspects of the species' natural history anticipating in many respects later more detailed studies.

One of the latest studies to be published should be cited at the outset. Young (1959) in his exhaustive morphological study of *P. setiferus* reiterated the generalized structure of the Penaeidae. This work is profusely illustrated and the text illuminates details which have often been obscurely presented in older works. Complexes such as the branchial apparatus and associated structures are clearly delineated, as are the skeletal, muscular, nervous, circulatory, and respiratory systems in general. The genital armature, of great taxonomic value, is treated briefly, and here the student must look to the works of Burkenroad (1934b, 1939) for details.

In 1956, Lindner and Anderson summarized work of the U.S. Bureau of Fisheries and the Fish and Wildlife Service in the 1930's and 1940's that had been presented in a series of shorter articles. Reference to this paper will lead the reader to earlier detailed studies.

Spawning of the white shrimp in the Carolinas probably begins in May and extends into September (Lindner and Anderson, 1956; Williams, 1955a); farther south in the Gulf of Mexico the season probably extends from March to September or October. Gunter (1950) suggested two periods of spawning (spring and fall) for Texas waters, but in the Carolinas there is probably only one.

Maturation of gonads has been studied in detail (King, 1948) in both males and females. In females, the stages of maturity can be judged macroscopically by color of the ovary. The earliest or undeveloped stage may last for an indeterminate period of time (Lindner and Anderson, 1956); the developing stage is judged to last a month or less. The succeeding yellow stage persists for 1 to 2 months, and the ripe, olive-drab colored ovaries become spent in less than a month.

Spent ovaries were found to revert to the yellow stage in a period of a few days and then to develop toward a ripened stage again in 2 or 3 months. A large female is estimated to produce a half million to a million eggs at a single spawning (Anderson, King, and Lindner, 1949).

It was thought that studies of the ovary would lead not only to discovery of spawning grounds but also to knowledge of how many times a female shrimp might spawn, and to the approximate age and length of life of the shrimp. Such hopes were incompletely realized. The likelihood of multiple spawning and absence of permanent scars or walled-off areas in the ovary precluded aging by this method. It is possible, but not proved, that a shrimp can spawn more than once in a season. Occurrence of ripe females suggests that spawning in Louisiana takes place offshore in depths greater than 4.5 fathoms, probably between 5 and 17 fathoms. Heegaard (1953) reported occurrence of spawning 6 or more miles from shore in from 10- to 15-fathom water in Texas. The exact location of spawning grounds off the Carolinas remains unknown.

Developmental stages of the white shrimp were elaborated in detail by Pearson (1939), based on plankton tows off the Mississippi River Delta and the coasts of South Carolina, Georgia, and Florida, and on rearing experiments with material taken from plankton catches at St. Augustine Inlet, Fla. (The eggs of penaeids are not carried on the pleopods of the females as in other decapods, but are broadcast.) In this study, few eggs were found, but this circumstance was attributed to the fact that the eggs are demersal, hence, hard to capture, and perhaps deposited chiefly beyond the area sampled. Of the material available for rearing, 5 of 15 eggs hatched within 24 hours after capture. Developmental stages prior to hatching were described, and, following hatching, five naupliar, three protozoeal, two mysis, and a series of postlarval stages were described. Pearson thought it likely that though the larvae are more or less at the mercy of currents in the environment, they still are capable of considerable independent movement. From the spawning place at sea, a great number of the larvae move inshore and enter estuaries at about the second postlarval stage (7 mm. total length), and it is at this stage that they abandon planktonic for a benthonic existence. The length of larval existence from time of hatching to entrance into estuaries was judged to be about 2 or 3 weeks.

Heegaard (1953), studying wild populations of larval white shrimp, and Johnson and Fielding (1956), studying populations reared in captivity, gave somewhat different interpretations of this portion of development. Heegaard suggested that the number of molts in certain portions of the larval history may vary individually; Johnson and Fielding, while agreeing with Pearson's descriptions of stages, gave evidence for shorter time of development from hatching to first postlarva (about 2 weeks). They also gave evidence for very rapid growth of the young, 2.1 mm. and 1.7 mm. per day in different experiments under conditions of full feed. The same authors secured good growth in both high and medium salinities.

Bearden (1961) demonstrated that postlarval *P. setiferus* enter South Carolina sounds from June through September, a period similar to the supposed recruitment period in North Carolina (Williams, 1959).

Once in estuaries on so-called "nursery grounds" the young grow rapidly. Williams (1955a) estimated an average increase in length of 36 mm. per month (1.2 mm. per day), and other estimates of similar nature have been made (Gunter, 1956; Loesch, 1957). The young, which in the early part of their benthonic existence tend to seek the fresher, shallower portions of estuaries, move gradually into deeper, saltier water as they grow, and with approaching maturity they return to sea. Hoese (1960) suggested that migration to estuarine nursery grounds may not be essential to development in this species, but Gunter (1961) gave much evidence to the contrary. Most of the individuals that grow to maturity appear to live a year or a little longer. Some exceptional individuals in the deeper portion of the range may live to be about 2 years old. Mature females attain a larger size than mature males. Lindner and Anderson (1956) estimated that mature *P. setiferus* grow at a rate of about 20 mm. per month during the period March to October.

In addition to annual cyclic movements of larvae into estuaries, and subsequent movement of subadults back to sea, tagging experiments have indicated that *P. setiferus* may make coastwise migrations of considerable length. In their ana-

lysis of these experiments, Lindner and Anderson (1956) showed that in fall and winter, shrimp tend to move south along the Atlantic coast; in late winter and early spring, there is a return movement; and during late spring and summer, position of the population is relatively static. Large individuals are prone to move longer distances than small shrimp. The longest recorded southward movement was by a shrimp tagged at Beaufort, N.C., in October, and recovered 95 days later off Florida, 360 miles from the point of release. The greatest counter movement was from Cape Canaveral, Fla., in January, to South Carolina 168 days later, a distance of 260 miles.

Distribution of *P. setiferus* is not uniform, and this may be conditioned by a number of factors. These are usually thought to be salinity, temperature, and substrate. The young may utilize waters of somewhat lower salinity than the young of related penaeids (Burkenroad, 1934b; Williams, 1955a). Hildebrand and Gunter (1953) and Gunter and Hildebrand (1954) demonstrated a strong positive correlation between the white shrimp catch for a given year and total rainfall for that year and the 2 preceding years in Texas, high rainfall being followed by good catches. In colder portions of the year no young are found in inside waters, at least in the Carolinas (Williams, 1955a). *Penaeus setiferus* is usually found on a muddy substrate on trawling and nursery grounds (Springer and Bullis, 1954; Hildebrand, 1954, 1955), and in experimental tanks it has been shown to choose muddy substrates in preference to sandy or rocky bottoms even though it burrows to a lesser extent than its near relatives (Williams, 1958).

In recent years the subadult populations of white and other penaeid shrimp in estuaries have been exploited for fish bait. Studies of such fisheries have given more detail on migrations and density of population (Loesch, 1957) and on individual length-weight relationships (Chin, 1960).

Penaeus duorarum Burkenroad. Pink, spotted, brown spotted, or grooved shrimp

Figures 10–11

Penaeus brasiliensis: Hay and Shore [in part], 1918, p. 377, pl. 25, fig. 6.
Penaeus duorarum Burkenroad, 1939, p. 31, figs. 18, 19, 23, 25–27 (rev.).

Recognition characters.—Integument thin, polished, translucent. Carapace with a median carina continuous anteriorly with rostrum and extending nearly to posterior border of carapace, flanked on each side by a broad, rounded groove; posterior half of carina with a median longitudinal groove; anterior half arcuate, highest above orbit and with 9 or 10 sharp teeth; posterior tooth remote from others, anterior 6 or 7 on rostrum proper. Lower margin of rostrum wth two to three teeth (occasionally one); tip slender, horizontal or directed slightly downward, unarmed. Anterior margin of carapace with strong antennal spine on carina extending backward nearly to well-developed hepatic spine. Cervical groove extending halfway from hepatic spine to dorsal carina. A subhorizontal suture below hepatic spine, and a groove extending from near hepatic spine to near base of ocular peduncle. An orbital ridge behind eye.

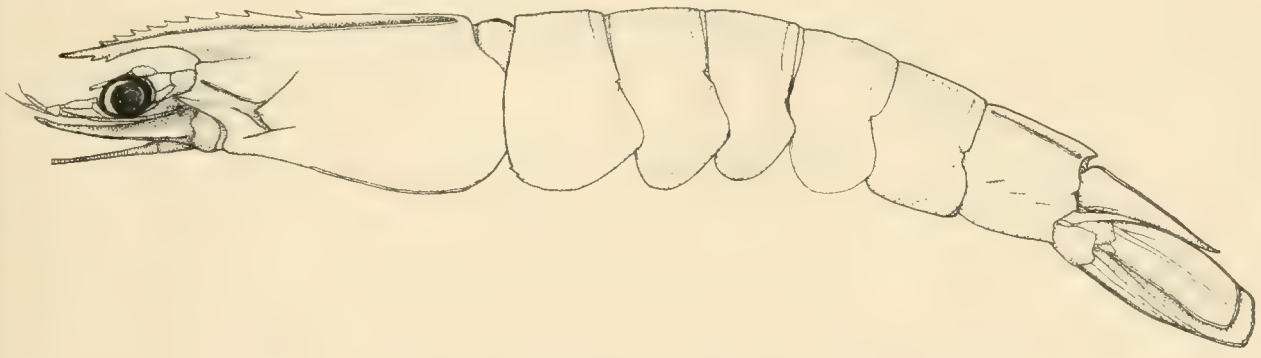

FIGURE 10.—*Penaeus duorarum* Burkenroad. Animal in lateral view with part of appendages removed, "Form A" from North Carolina; natural size.

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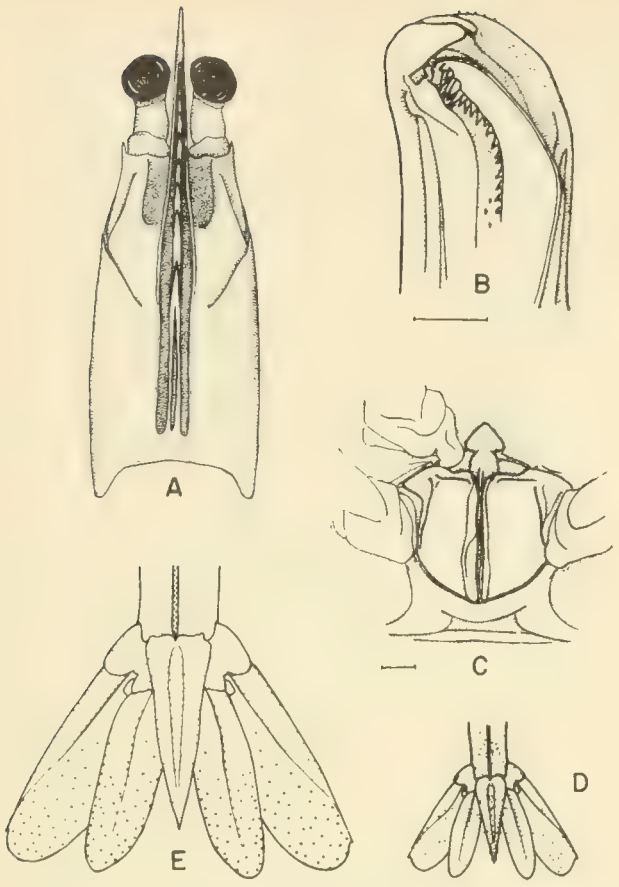

FIGURE 11.—*Penaeus duorarum* Burkenroad. A, carapace and eyes of animal in dorsal view, "Form A" from North Carolina, natural size; B, petasma of adult male, distal portion, view from right side; C, thelycum of adult female; B–C, 1 mm. indicated (after Burkenroad, 1939). Chromatophore distribution in tail fan (semi-diagrammatic) of D, 17 mm. juvenile, E, 32 mm. juvenile; D–E, approximately × 5 (after Williams, 1953).

Female with thelycum composed of two broad lateral plates, and a median plate. Posteromedian part of median plate of adult with a well-developed, short, longitudinal carina extending anteriorly toward roughly semicircular, concave anterior portion. Lateral plates produced medially to meet in midline, except variably divergent at anteromedian corners, thus exposing carina of median plate.

Abdomen with segments four to six carinate, carina of sixth ending posteriorly in a spine and flanked on each side by a narrow groove. Telson with deep median groove and an acuminate tip.

Petasma of male with distal ends of distoventral lobes curved medially, not projecting free of distolateral lobes; external edge of distoventral lobes with a series of 2 to 12, usually 4 to 7, small spinules; median or attached edge of distoventral lobes with a compact group of 6 to 16 large, long, sharp, curved spines; fold of distolateral lobe rather small and armed inconspicuously if at all.

Measurements.—Length of body: large male, 167 mm.; large female, 210 mm.

Variations.—Burkenroad (1939) divided the species into two "Forms," "A" and "B."

In "Form A" the dorsolateral grooves of the sixth abdominal segment usually are almost or entirely closed, though they may be open to a width of one-third the distance from their dorsal lip to the midline.

In "Form B" the dorsolateral grooves of the sixth abdominal segment are broadly open, their width being from one-half to more than equal the distance from their dorsal lip to the midline.

The rostrum is relatively shorter and deeper in old individuals than in young ones. It extends to the end of the basal antennular article in average-sized adults. The rostrum in *P. duorarum* is less sinuous and slender than in *P. aztecus*.

Color.—Juveniles and young adults from estuaries or oceanic water near shore are usually gray, reddish brown or bluish gray of various shades, with a more or less distinct spot of darker color at the pleural juncture of the third and fourth abdominal segments. In juveniles or young adults, this spot and other bandings may be gray, blue gray, blue, or purplish. The tail fan is nearly transparent and edged with blue. In older individuals, especially from deeper oceanic water, the colors tend to be red, pinkish, blue gray or nearly white. The abdominal spots are usually red (Broad, 1950) or lacking entirely. Detailed coloration of the young has been given by Williams (1953).

Habitat.—Estuaries and inner oceanic littoral, predominantly on sand, shell-sand or coral-mud bottom from water's edge to 28 fathoms; rarely 40 to 200 fathoms (U.S. Fish and Wildlife Service, 1960).

Type locality.—Off Alabama (*Atlantis* station 2813, roughly lat. 30° N. long. 88° W.), 19 fathoms.

Known range.—Chesapeake Bay through Gulf of Mexico and West Indies to Brazil; Bermuda; West Africa, from Mauritania to Angola.

"Form A," Chesapeake Bay to Campeche, Mexico; Bermuda. "Form B," Cuba through West Indies to Brazil; West Africa.

Remarks.—Penaeus duorarum, one of the western Atlantic littoral penaeids extensively utilized for food, is caught in commercial quantities throughout much of its geographic range (North Carolina to Nicaragua and perhaps Brazil (Lindner, 1957)). Distribution of this species is by no means uniform, consequently the fisheries are concentrated at diverse points, some of these being North Carolina, Key West, Fla., and Campeche Banks, Mexico, with the latter two being by far the largest. At other points in the range, the species is not abundant enough to support a fishery worthy of note.

A number of recent studies, especially in Florida, have greatly enhanced our knowledge of this species but only a brief summary is appropriate here.

In North Carolina, roe-bearing females and mature males appear in commercial catches from the ocean near Beaufort Inlet in May (Broad, 1950; Burkenroad, 1949; Williams, 1955a) and they continue to occur into July. Mature ovaries are blue-green in color. One spawning season a year is indicated for this, the northernmost breeding population of the species. There is strong evidence that this population is endemic.

In Florida, Cummings (1961) found stages of maturation in the ovaries of *P. duorarum* females similar to those in *P. Setiferus;* i.e., the ovary passing through a flaccid undeveloped stage, a developing stage containing larger ova, a nearly ripe stage in which the ovary is large, visible from the outside and glaucous in color, and a ripe stage in which the ova contain characteristic rodlike refractive bodies, and finally a difficult-to-determine spent stage. The highest rate of spawning was judged to extend from April through July, a period comparable to that in North Carolina, but ripe and nearly ripe females were found at other times of year as well (see also Eldred, Ingle, Woodburn, Hutton, and Jones, 1961). Cummings indicated that multiple spawning probably occurs. Eldred, Ingle, Woodburn, Hutton, and Jones (1961) postulated that mating behavior is possibly related to migratory behavior and that spawning is initiated at minimal bottom temperatures of 23.9° C. (see also Cummings, 1961). They suggested that annual temperature ranges within certain poorly understood, but not fatal, limits may have a controlling influence on population size in the following year.

The egg and larval stages of *P. duorarum* were described in detail by Dobkin (1961) from material taken from the Dry Tortugas fishing grounds. Viable, yellow brown, opaque eggs, 0.31–0.33 mm. in diameter, were obtained from mature females spawning in the laboratory. The act of hatching required 2 to 3 minutes. Dobkin described five naupliar, three protozoeal, three mysis, and a number of postlarval stages. The naupliar and first protozoeal stages were reared in aquaria, but remaining stages were taken from plankton.

Postlarvae of *P. duorarum* have been distinguished from those of *P. aztecus* by Williams (1959), and more fully described by Dobkin (1961). The recruitment period in North Carolina, extending from late May to November, agrees well with the occurrence of ripe adults in the fishery prior to and during the early part of this period, and it also suggests that movement and development time of larvae is about the same as that found in *P. setiferus* (i.e., 2 or 3 weeks). Bearden (1961) found a few postlarval *P. duorarum* from May through September in South Carolina.

Once on the nursery grounds in estuaries, the young undergo rapid growth. Williams (1955a) estimated an average increase in length of young shrimp at 52 mm. per month (about 1.8 mm. per day) for warmer months. More recent work shows that this estimate may be too high. Eldred, Ingle, Woodburn, Hutton, and Jones (1961) found that pink shrimp spawned in late March or April could reach lengths of 45–65 mm. by July, while those spawned in May could reach lengths of 25–35 mm. by July. Iversen and Jones (1961) showed that a 103-mm. shrimp will grow 7 mm., a 130-mm. shrimp will grow 5 mm., and a 153-mm. shrimp will grow little or none in a month in either summer or winter. Eldred, Ingle, Woodburn, Hutton, and Jones (1961) estimated that a 140-mm. shrimp is about 1 year old and that on such basis shrimp measuring 200 mm. in

length are approximately 2 years old. Most individuals that grow to maturity live a year or longer. Adult females attain a larger size than adult males (various authors).

The young shrimp tend to seek shallower, often somewhat fresher, portions of the estuaries in the early part of their benthonic existence, and with increasing size move gradually into deeper, saltier water as they grow; finally, with approaching maturity they return to sea. This general pattern of movement may best be taken as a model which is variously complicated in different parts of the species' range. In North Carolina, and perhaps elsewhere (Iversen and Idyll, 1960; Eldred, Ingle, Woodburn, Hutton, and Jones, 1961) many of the juveniles present in the sounds in fall do not return immediately to sea but linger in the estuaries over winter. Here they are often subjected to quite low temperatures (4° C.) and in severe winters nearly all of this overwintering population may be killed. Normally they survive the winter, but because they are relatively inactive in the cold, they grow little, at least in North Carolina (November–April estimated average increase in length, 7.5 mm. per month). Rising springtime temperatures induce increased activity and feeding, resulting in resumption of rapid growth and an ensuing spring migration to sea in May and June. In North Carolina, this migrating population is large enough to create a sizable late spring fishery.

In Texas (Hildebrand, 1955) and Florida (Higman, 1952) young of *P. duorarum* are especially abundant in grassy areas of estuaries where salinities are 20 °/₀₀ or more. This is true of some areas in North Carolina, and the young are also concentrated most heavily in areas where there is a possibility of tidal transport (Williams, 1955b).

Tagging experiments to determine movements of this species have been restricted to waters off southern Florida. Iversen and Idyll (1960) and Iversen and Jones (1961) demonstrated a general northwestward movement for shrimp tagged on the fishing grounds west of Key West and suggested that small shrimp move from shallow water at the end of the Florida peninsula to the Tortugas fishing grounds.

Distribution of *P. duorarum* may be limited by the same factors that influence *P. setiferus;* i.e., salinity, temperature, and substrate. Hildebrand (1954, 1955) and Springer and Bullis (1954) emphasized the fact that *P. duorarum* fisheries are located in areas where the bottom is composed of calcareous muds and sands or mixtures of mud and sand. (This species usually burrows in the substrate in the daytime and is most active at night (various authors).) Laboratory experiments have shown that subadult *P. duorarum*, when allowed a free choice of sand, shell-sand, loose peat, muddy sand or sandy mud, tend to choose shell-sand with a somewhat lower preference for loose peat (Williams, 1958). In shell-sand the animals were often completely buried, and could be observed only after being dug out. The experiments confirmed observations on the correlation of location of fisheries with bottom type in the Gulf of Mexico and in North Carolina.

The fact that *P. duorarum* alone, of the three commercially abundant species of shrimps, is able to overwinter in estuaries in the northern part of its breeding range has suggested that it is better able to withstand a combination of low salinity and temperatures because of superior osmoregulatory abilities at low temperature. Preliminary studies have shown that *P. duorarum* is better able to regulate its internal fluids at low temperatures than its close relative *P. aztecus*, but regulatory ability of both species is impaired when temperatures are lowered to about 8° C., and survival of both species is better in moderate to high salinities at low temperatures (Williams, 1960). Eldred, Ingle, Woodburn, Hutton, and Jones (1961) considered that the depth to which the species may burrow in cold weather (6 inches) may protect it from sudden cold snaps.

Penaeus aztecus Ives. Brown or grooved shrimp

Figure 12

Penaeus brasiliensis aztecus Ives [in part], 1891, p. 190.
Penaeus brasiliensis: Hay and Shore [in part], 1918, p. 377.
Penaeus aztecus: Burkenroad, 1939, p. 34, figs. 20, 21, 24, 28–33 (rev.).

Recognition characters.—Integument thin, polished, translucent. Carapace with a median carina continuous anteriorly with rostum and extending nearly to posterior border of carapace, flanked on each side by a broad, rounded groove; posterior half of carina with a median longitudinal groove; anterior half arcuate, highest above orbit and with 9 or 10 sharp teeth; pos-

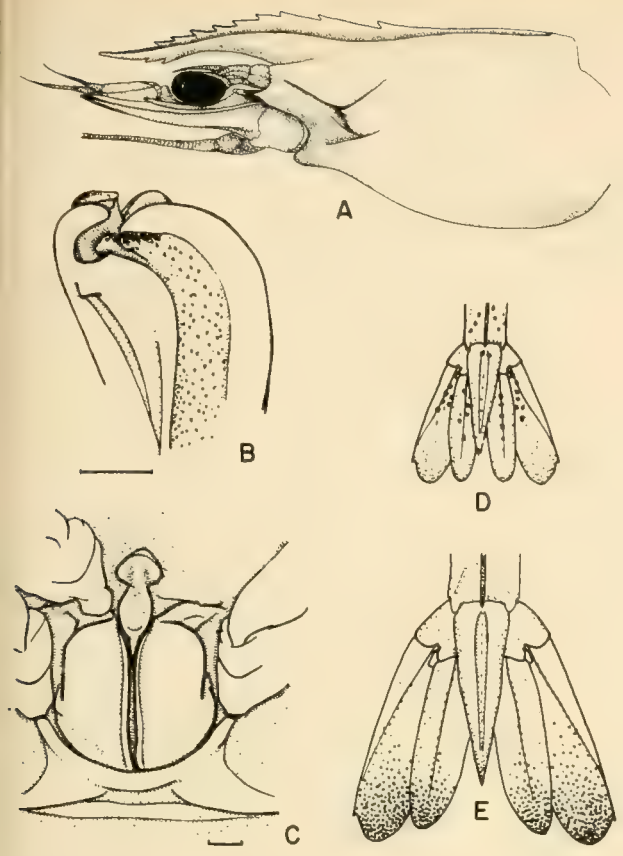

FIGURE 12.—*Penaeus aztecus* Ives. A, anterior portion of animal in lateral view, "Form A" from North Carolina, natural size; B, petasma of adult male, distal portion, view from right side; C, thelycum of adult female; B–C, 1 mm. indicated (after Burkenroad, 1939). Chromatophore distribution in tail fan (semidiagrammatic) of D, 17 mm. juvenile, E, 32 mm. juvenile; D–E, approximately × 5 (after Williams, 1953).

terior tooth remote from others, anterior 6 or 7 on rostrum proper. Lower margin of rostrum with two or three teeth, tip slender, horizontal, or directed slightly upward, unarmed. Anterior margin of carapace with strong antennal spine on carina extending backward nearly to well-developed hepatic spine. Cervical groove extending halfway from hepatic spine to dorsal carina. A subhorizontal suture below hepatic spine, and a groove extending from near hepatic spine to near base of ocular peduncle. An orbital ridge behind eye.

Female with thelycum composed of two broad lateral plates and a median plate. Posteromedian part of median plate variably ovate-acuminate in outline with tip raised into a short posterior carina diverging anteriorly into raised margins. Ventral surface concave; broad anterior end of posterior part merging into concave, triangular or semicircular anterior portion. Lateral plates produced medially to meet in midline except diverging to expose median plate.

Abdomen with segments four to six carinate, carina of sixth flanked on each side by a narrow groove. Telson with deep median groove and an acuminate tip. Petasma of male with distoventral lobes not projecting free of distolateral lobes; with several compact series of short, crowded spines near distal ends; a fold of free margin of distolateral lobe beyond end of distoventral lobe bearing moderate spinose armature.

Measurements.—Length of body: large male, 162 mm.; large female, 211 mm.

Variations.—Burkenroad (1939) divided this species into "Forms," "A," "B," and "C." The chief differences are summarized here.

In "Form A," the grooves lateral to the dorsal carina are well defined posteriorly and are distinctly broader than the carina. The carina is distinctly and continuously grooved. The dorsolateral grooves of the sixth abdominal segment are broadly open, their width "being from three-fourths to equal the interval between their dorsal lip and the midline."

In "Form B," the grooves lateral to the dorsal carina are usually much narrower than the carina and tend to be ill defined posteriorly. The dorsolateral grooves of the sixth abdominal segment "range up to one-half as broad as the interval between their dorsal lip and the midline, and the dorsal lip is frequently low and ill defined."

In "Form C," the grooves lateral to the dorsal carina are much as in "Form A," but the carinal groove is shallow and frequently interrupted by plane intervals. The dorsolateral grooves of the sixth abdominal segment are extremely narrow, "their width less than a third of the interval between their dorsal lip and the midline, and are sometimes entirely closed."

The rostrum is relatively shorter and deeper in old individuals than in young ones. In unworn adults, it reaches to or beyond the middle of the third antennular article. In young adults, it may reach the end of the antennal scale. The rostrum

in *P. aztecus* is more sinuous and slender than in *P. duorarum*.

Color.—Juveniles and young adults from estuaries or oceanic water near shore are usually brown or grayish brown, occasionally with darker spots or faint concentrations of chromatophores at the pleural articulations. Individuals from deeper water are light orange (Burkenroad, 1939). The tail fan is darkened distally and in adults is edged with purple to reddish purple. Detailed coloration of the young has been given by Williams (1953).

Habitat.—Estuarine and oceanic littoral, predominantly on mud bottom from water's edge to 45 fathoms; rarely to 89 fathoms.

Type locality.—Veracruz, Mexico.

Known range.—New Jersey (occasionally to Marthas Vineyard, Mass.) through Gulf of Mexico and West Indies to Uruguay.

"Form A," New Jersey to Campeche, Mexico.

"Form B," Florida through West Indies; Panama to Rio de Janeiro, Brazil.

"Form C," Pernambuco, Brazil, to Montevideo, Uruguay.

Remarks.—*Penaeus aztecus*, the third of the littoral penaeids abundant enough to be utilized profitably for food, is also fished commercially throughout much of its range (North Carolina to Brazil), and total landings for this species now outstrip the other two combined. When the U.S. Bureau of Fisheries began research on the natural history of *P. setiferus* in the 1930's, few grooved shrimp were sold, but with the advent of increased market, larger trawlers, and discovery of large concentrations of both *P. duorarum* and *P. aztecus* in different localities than had formerly been fished, the latter species were extensively utilized. Conversely, in recent years it is also possible that there has been a decline in abundance of *P. setiferus* throughout much of its range (various authors). Tremendous quantities of *P. aztecus* are now landed in the western Gulf of Mexico.

Prior to Burkenroad's revision (1939) of the grooved shrimps of the western Atlantic, three currently recognized species were lumped under the name *P. brasiliensis*. Biological data taken prior to that time on these species, never so extensive as those for *P. setiferus*, cannot now be assigned with certainty to any single species. However, taking into consideration the locations where research was done, as well as modern knowledge of species distributions, it is probable that most of those data on grooved shrimps apply to *P. aztecus* (see also Pearson, 1939).

Maturation of gonads in *P. aztecus* probably parallels the process as understood in *P. setiferus*, although few data are recorded on this subject. Broad (1950) described maturing ovaries found in August as opaque white, yellow, tan, or gray in color. Burkenroad (1939), working in Louisiana, noted that whereas the proportion of males to females in *P. aztecus* near shore was about 1 to 1, this ratio progressively changed in samples farther from shore, in deeper water, to a ratio of 1 to 2 in water 50–70 fathoms deep. Moreover, the females in deep water were much larger than the males, a characteristic shown also by the related *P. setiferus* and *P. duorarum* and young adult populations of all three species inshore. Burkenroad attributed the size disparity of these large offshore individuals to greater length of life among females. Knowledge that impregnated females occurred only beyond 10 fathoms, together with the fact that mature (and possibly spent) ovaries were found only in individuals beyond these depths at various times of year, led him to propose that the females spawned a number of times during an ill-defined spawning season.

Williams (1959) favorably assessed Pearson's (1939) determination of *P. brasiliensis* (unfortunately misspelled "*braziliensis*," in Williams) as most probably *P. aztecus*, and proceeding on the basis of Pearson's distinguishing characters was able to separate *P. duorarum* and *P. aztecus* postlarvae in the plankton in North Carolina. Postlarvae of the latter were found entering the sounds from October to May, with peak recruitment from late March to early April. Bearden (1961) found peak recruitment to occur in February and March in South Carolina. These patterns agreed well with collections of juveniles (Williams, 1955a) in which recruitment began in mid-April and continued through the summer. A long winter spawning season supplies postlarvae to the Carolina sounds, but fall and midwinter recruits are apparently killed by cold weather for they never progress beyond postlarvae

in the samples taken. Pearson found postlarvae in Louisiana in all months of the year, but in no more than 11 months of any calendar year. The usual recruitment period seemed to run from late January to late summer.

Gunter (1950) found young brown shrimp in Texas bays most common in spring and fall with low abundance in late summer and winter.

Evidence indicates that *P. aztecus* has an extended spawning season which probably varies in different parts of the range. The spawning site is probably deeper and farther from shore than in *P. setiferus* and *P. duorarum.*

Young *P. aztecus* enter estuaries as postlarvae, migrate to shallow, often low-salinity water, and undergo a remarkably rapid growth in the warmer months. In North Carolina, the juveniles increase in mean length by an estimated 46 mm. per month (1.5 mm. per day, Williams, 1955a). As they grow, they gradually move to deeper, saltier water and eventually return to sea. In North Carolina, and perhaps elsewhere, *P. duorarum* and *P. aztecus* use essentially the same nursery grounds over large areas of the sounds; however, the seasons of recruitment to and occupation of these areas is staggered in such a manner that the two species are rarely on common ground (Williams, 1955a, b). The growing bait fisheries for estuarine shrimp in recent years have given impetus to studies in Alabama and Texas. Additional information on migration (Loesch, 1957) and studies on length-weight relationships (Chin, 1960) have resulted from this work.

Again, distribution of *P. aztecus* is usually thought of as limited by such factors as salinity, temperature, and substrate. Hildebrand (1954, 1955) and Springer and Bullis (1954) stated that the commercial fishery for this species in the Gulf of Mexico was confined largely to bottoms of terrigenous silt. (Like *P. duorarum*, *P. aztecus* is a burrower, and in many areas is more active in open water at night than in daytime.) In experimental tanks, when given a choice of sand, shell-sand, loose peat, muddy sand and sandy mud, *P. aztecus* was found to favor loose peat, sandy mud and muddy sand, closely paralleling *P. setiferus* in choice of bottom type (Williams, 1958). The experiments confirm field observations on habitat along the coast of North Carolina and in the Gulf of Mexico.

Penaeus aztecus has been found to have a less efficient osmoregulatory mechanism at low temperatures in low salinities than *P. duorarum* (Williams, 1960). For this reason, it is probably not so resistant to wintertime conditions in estuaries as *P. duorarum.*

Genus ***Parapenaeus*** Smith, 1886

Burkenroad, 1934b, p. 107.

Parapenaeus longirostris (Lucas)

Figures 13–15

Peneus longirostris Lucas, 1849, p. 46, pl. 4, fig. 6.
Parapenaeus politus: Hay and Shore, 1918, p. 379, pl. 25, fig. 7.
Parapenaeus longirostris: Burkenroad, 1934b, p. 108 (rev.).—1939, p. 53.

Recognition characters.—Integument smooth, not setose. Carapace with a low carina extending almost to posterior margin and bearing a spine some distance behind rostrum. Rostrum arched: distal half deflexed, tip somewhat upturned, extending to or beyond distal edge of eye; dorsal margin with usually seven teeth diminishing in size anteriorly; ventral margin heavily ciliated. Hepatic, antennal, and branchiostegal spines well developed; later spine placed a little behind margin of carapace. A rectangular toothlike eminence at orbital angle. A shallow groove extending from behind eye almost to posterior edge of carapace, and another, extremely faint, running upward from inferior margin at base of second pair of legs. Basal antennular article with a spine on ventromedian margin distally.

Thelycum of female composed externally of a triangular plate with obtuse apex on 13th somite (base of 4th leg); 14th sternite raised anteriorly, with low relief posteriorly; lateral ridges with nearly straight but divergent medial borders separated by nearly plane, broad medial groove; lateral border of ridges ornately curved to fit contour of adjacent coxae and 13th sternite.

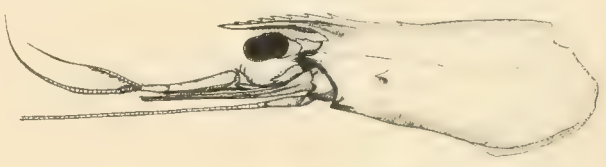

FIGURE 13.—*Parapenaeus longirostris* (Lucas). Anterior portion of animal in lateral view, × 3.

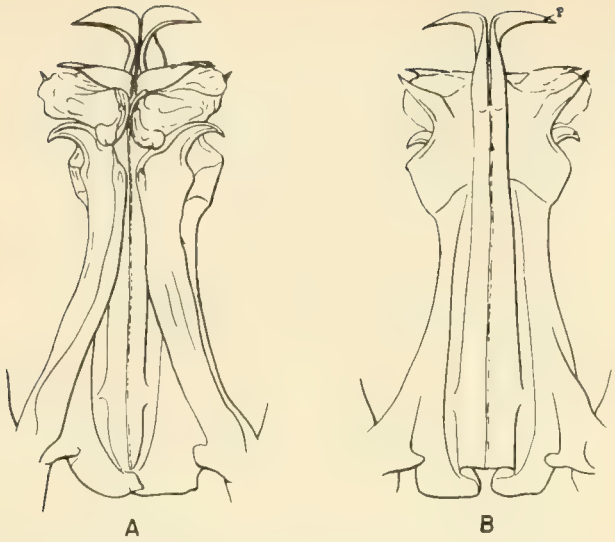

FIGURE 14.—*Parapenaeus longirostris* (Lucas). Petasma of male, A, ventral view; B, sternal view (after Heldt, 1938).

FIGURE 15.—*Parapenaeus longirostris* (Lucas). Thelycum of female; A, external plate of somite 13; B, internal structure showing sacs extending into somite 14 (after Heldt, 1938).

Petasma of male with each half terminating in a dorsomedian spinelike projection with a fleshy distomedian lobe at base; proximal to latter, a broad lateral spine with a fleshy distolateral lobe at base continuous with distomedian lobe but not projected laterally as a spoutlike horn as in *Xiphopeneus;* finally, still further proximally a spinelike distoventral projection partially covered by a medial distoventral flap.

Abdomen with fourth, fifth, and sixth segments carinate, carina ending on each segment in a small tooth. Sixth segment a little more than twice length of fifth. Telson tapering to a sharp point, furrowed above, with a slender spine on each side near tip.

Measurements.—Western Atlantic population: length of body, 104 mm. Mediterranean population: length of body, 165 mm.

Variations.—European examples of the species attain a greater size than do American forms. The length of the rostrum varies with age, becoming relatively longer with variable development of an unarmed tip in large individuals. The sixth abdominal segment is relatively shorter in large than in small individuals.

Color.—Eyes green; body and appendages mottled with red and pale translucent areas; uropods with exopod and distal half of endopod deep red (Burkenroad, 1934b).

Habitat.—Soft mud or muddy sand bottom (Heldt, 1954); 15 to 180 fathoms or more in western Atlantic (Burkenroad, 1934b, 1939); 20 to 250 fathoms in Mediterranean (Heldt, 1954, 1955).

Type locality.—Algiers and Cap-Matifou, Algeria.

Known range.—Marthas Vineyard, Mass., to Gulf of Mexico off Florida, Louisiana, and Yucatan; Gulf of Paria off Venezuela; coast of Portugal to Morocco; Mediterranean Sea from Spain to Asia Minor.

Remarks.—Though this species occurs on both sides of the Atlantic, it has been studied in detail chiefly in the European portion of its range. The European population is composed of larger individuals than the American population (Burkenroad, 1934b) and because of its size and abundance is commercially exploited off the coast of Tunisia (Heldt, 1954). The American population is also quite abundant in the northern Gulf of Mexico (Burkenroad, 1939).

It is possible that this species lives beyond the 100-fathom depth off the Carolinas, but because it is known to move into shallower water in parts of its range it is included here. Heldt (1938) stated that the depth distribution starts at about 30 fathoms, but usually extends from 55 to 200 and more fathoms. She described characteristic features of what she termed the "fonds à Parapenaeus" in the Mediterranean Sea (1954).

The developmental stages of this species have been treated in detail by Heldt (1938) from the Mediterranean and in somewhat lesser detail by Pearson (1939) from the northern Gulf of Mexico.

Heldt described cleavage stages of the egg, formation of the embryo, 8 naupliar, 3 protozoeal, 14 mysis stages, and the first postlarval stage. Pearson found protozoeal, mysis, and postlarval stages principally during July off South West Pass, La.; and usually a complete set of larval stages was taken in a single plankton collection. A single mysis was taken south of Barataria Pass, La., in May and a single first protozoea at Fort Pierce, Fla., in January.

Genus *Penaeopsis* Bate, 1881

Bate, 1881, p. 182.

Penaeopsis goodei (Smith)

Figures 16–17

Parapenaeus goodei Smith, 1885, p. 176.
Penaeopsis goodei: Verrill, 1922, p. 44, pl. 15, figs. 1A–1Aiv; pl. 16, fig. 3.—Burkenroad, 1934a, p. 15, figs. 2, 3 (rev.).

Recognition characters.—Carapace and abdomen covered with rather stiff, plumose hairs. Carapace about as wide as deep and very little compressed anteriorly. Rostrum rising obliquely above level of dorsum, shorter than carapace proper and armed above with 8 to 10 teeth in front of orbital margin; a sharp gastric tooth behind rostral carina. Antennal, hepatic, and branchiostegal spines well developed; a rectangular toothlike eminence at orbital angle; grooves inconspicuous. Eyes large, reniform, flattened above. Antennular flagella subequal in length and about as long as second article of peduncle. Antennal scale reaching to tip of antennular peduncle; distal portion of thickened outer margin armed above with series of minute spines directed obliquely forward and outward.

Third maxilliped, first and second legs armed with basal spines. A small distal spine on ventral side of ischium of first leg. A pair of long, slender spines arising from sternum between second legs.

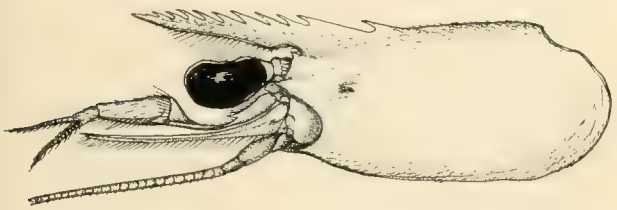

FIGURE 16.—*Penaeopsis goodei* (Smith). Anterior portion of animal in lateral view.

FIGURE 17.—*Penaeopsis goodei* (Smith). A, petasma of male in ventral view, approximately × 9.5; B, petasma in ventral view, distal portion with right external piece removed, approximately × 14 (after Burkenroad, 1934a).

Thelycum of female composed of an anterior flattened oval portion with a slender anterior median spine on 13th somite (between 4th leg), and a short broad, posterior portion on 14th somite connected to preceding structure by a less elevated median prominence flanked by an irregular bulbous enlargement on each side. Petasma of male exceedingly complicated and asymmetrical; left side irregularly folded longitudinally, projecting proximally in a curved process beyond right half and to right of median line, and extending distally in an irregular process; right side enlarged distally and divided into several irregularly curved processes projecting beyond left appendage, and partially covered posteriorly by a thin spoon-shaped lamella arising at their bases.

Abdomen with third to sixth segments carinate dorsally; carina of fourth and fifth narrowly cleft at posterior margin. Telson considerably longer than sixth segment; rounded and obscurely grooved above; regularly tapered; armed with a long spiniform process at each side of acute tip, and three pairs of movably articulated spines in front of lateral spines, posterior ones largest.

Measurements.—Length of carapace including rostrum: male, 19 mm.; female, 21 mm.

Habitat.—Surface to 180 fathoms.

Type locality.—Bermuda.

Known range.—Between Capes Hatteras and Lookout, N.C., through Caribbean Sea and West Indies to Surinam; Bermuda.

Remarks.—Larval stages from Bermuda that probably belong to this species were described by Gurney (1943b). From observations at Bermuda, Wheeler (1937) described characteristic swarming of this species at about an hour after sunset, with monthly maxima on the 2d and 26th days of the lunar month.

Genus ***Xiphopeneus*** Smith, 1869

Burkenroad, 1934b, p. 102.

Xiphopeneus kroyeri (Heller)

Figures 18–20

Peneus kroyeri Heller, 1862, p. 425, fig. 51.
Xiphopeneus kroyeri: Burkenroad, 1934b, p. 103, fig. 12 (rev.).—Schmitt, 1935a, p. 132, fig. 5.—Holthuis, 1959, p. 70, fig. 7.

Recognition characters.—Carapace and abdomen smooth. Rostrum laterally compressed, sinuous, armed with usually five dorsal teeth at base, styliform tip greatly elongated beyond antennal scales and varyingly elevated. Carapace with a single epigastric tooth behind rostral series on rounded postrostral carina extending from base of rostrum to near posterior border; no transverse suture in adults; anterior cervical groove reaching anterior margin and continuous with branchiocardiac groove reaching almost to posterior border; hepatic and antennal spines present. Antennal flagella much longer than body; antennal scale extending beyond tip of antennular peduncle. Inferior antennular flagellum up to 50 percent length of antenna. Exopodites of second and third maxillipeds slender.

Last two pairs of legs elongate, flagelliform, with dactyls many jointed.

FIGURE 18.—*Xiphopeneus kroyeri* (Heller). Anterior part of animal in lateral view, approximately × 3.2 after Holthuis, 1959).

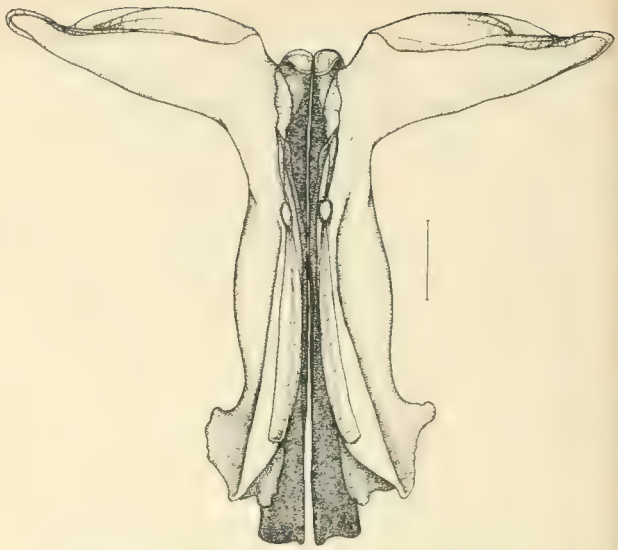

FIGURE 19.—*Xiphopeneus kroyeri* (Heller). Petasma of adult male, ventral view, 1 mm. indicated.

FIGURE 20.—*Xiphopeneus kroyeri* (Heller). Thelycum of female, filled sperm sacs showing through abdominal integument (after Burkenroad, 1934b).

Fourth to sixth abdominal segments carinate, with small dorsal tooth at posterior end of carina on each segment; sixth segment with carina high and deep. Telson tapering to acute tip.

Petasma of male with distolateral corners greatly produced as hornlike projections, open along distal margins on thoracic face. Thelycum of female externally appearing as an unpaired plate extending forward from last thoracic somite.

Measurements.—Length of body: 127 mm.

Variations.—The rostrum is somewhat longer in females than in males, and varies with age. In individuals with carapace length under 9 mm., the rostrum is shorter than the carapace, but beyond this size it is usually longer than the carapace.

Color.—Whitish, ventral part yellowish, occasionally with yellow over whole body but most

distinct ventrally; dark chromatophores scattered throughout and when expanded giving animal a grayish cast; tips of rostrum and flagella reddish; legs pinkish or yellowish orange; pleopods and uropods yellowish at base, pink distally; telson and sixth abdominal segment sometimes pink (Holthuis, 1959).

Habitat.—This species lives in a narrow zone along shore, and at times in the lower portion of estuaries (Gunter, 1950; Holthuis, 1959), from 2.5 to 20 fathoms, rarely to 24 fathoms (Burkenroad, 1939; Gunter, 1950).

Type locality.—Rio de Janeiro, Brazil.

Known range.—Between Capes Hatteras and Lookout, N.C., through Gulf of Mexico and Caribbean Sea to near Santos, São Paulo, Brazil; Pacific coast variety (*X. riveti*, see Burkenroad, 1934b) from Mexico to northern Peru.

Remarks.—This species is of commercial importance in the southern United States (Weymouth, Lindner, and Anderson, 1933; Hildebrand, 1954), and of great importance in South America (Lindner, 1957; Higman, 1959), especially along the northeast coast where it dominates the nearshore fishery and the young dominate the coastal nursery areas, perhaps offering serious competition to other penaeids.

No detailed study of the ecology of this species has been made. Burkenroad (1949) observed ripe or nearly ripe females off North Carolina in May, and Gunter (1950) found them along the Texas coast in June. Vieira (1947), in a study on maturation, found mature females off São Paulo, Brazil, from November to January.

Gunter (1950) studied a population ranging in size from 28 to 127 mm. total length. He found a population mode of 38 mm. total length in October but no definite modes in other months. The species was most abundant in fall. Gunter pointed out that the species does not customarily live in bays, even though it lives in shallow water close to the Texas shore. The young may enter the lower end of Texas bays (21.2–30.7 °/₀₀), but most individuals were found in the Gulf of Mexico in a salinity range of 29.7 to 35.2°/₀₀. Similar salinity tolerances were implied by Lindner (1957) and noted by Holthuis (1959). Though the South American shrimp are caught in estuaries and rivers, the penetration into these areas is greatest in dry seasons. Both Lindner and Holthuis gave data on the fisheries and processing methods.

Genus *Trachypeneus* Alcock, 1901

Burkenroad, 1934b, p. 94.

Trachypeneus constrictus (Stimpson)

Figure 21

Penaeus constrictus Stimpson, 1871b, p. 135.
Trachypeneus constrictus: Hay and Shore, 1918, p. 378, pl. 25, fig. 9.—Schmitt, 1935a, p. 131.

Recognition characters.—Dorsal region of carapace with fine, short, appressed setae; branchial region of carapace and last two abdominal segments variably pubescent; abdomen smooth proximally. Carapace carinate except for short stretch near posterior border; a spine behind base of rostrum; antennal and hepatic spines well developed; a rectangular toothlike eminence at orbital angle; lateral groove extending about three-fifths length of carapace; anterolateral angle truncate. Rostrum reaching to about middle of second segment of antennal peduncle, directed slightly upward; upper margin usually slightly arched and bearing usually seven to nine equidistant teeth diminishing in size toward tip. Eyes large, reniform. Antennular peduncle pubescent above, extending slightly beyond antennal scale; flagella shorter than carapace. Third maxilliped, first and second legs with basal spines.

Abdomen carinate from fourth to sixth segment. Telson with two rounded carinae above; tapering to a short acuminate tip, armed on either side with a short spine.

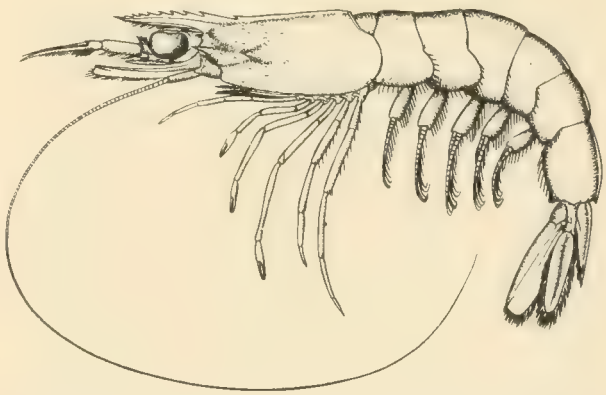

FIGURE 21.—*Trachypeneus constrictus* (Stimpson). Animal in lateral view, approximately × 1.5 (after Verrill, 1922).

Thelycum of female with anterior margin of median plate and lips of transverse groove evenly rounded, notched in middle; lateral flaps of last thoracic somite overlapping median plate; rib supporting expanded median plate extending anteriorly and sharply set off from anterior ventral margin of plate; ventral surfaces pubescent. Sternal elevation between coxae of fifth leg of male with lateral margins indented setting off posterior portion from broad anterior basal portion; petasma with distolateral corners greatly produced as hornlike projections.

Measurements.—Length of body: 92 mm.

Color.—Translucent with purplish-gray blotches; appendages pink.

Habitat.—Primarily sand or mud and shell bottom in high-salinity water; shallow water to 30 fathoms.

Type locality.—Beaufort, N.C.

Known range.—Tangier Sound, Chesapeake Bay, to Texas; Bermuda; Puerto Rico and Sombrero Island; Surinam.

Remarks.—Eldred (1959) reported *T. constrictus* as common in the Tortugas area of Florida where, along with its near relative, *T. similis*, it makes up about 7 percent of the annual commercial catch. It probably contributes more to catches in deeper water than to catches in the area sampled. Gunter (1950) stated that *T. constrictus* was rarely taken in coastal bays of Texas, being largely confined to water above 30‰. In littoral waters, ripe females were taken in September and small specimens (about 29 mm. total length) in March.

Burkenroad (1939) remarked that *T. constrictus* might be restricted largely to sandy bottom, and Hildebrand (1955) suggested a distribution possibly correlated with bottom type, but did not specify the type.

The early developmental stages of *T. constrictus* were treated by Pearson (1939). All larval and postlarval stages were pieced together by successful rearing techniques coupled with plankton catches at St. Augustine Inlet, Fla. Descriptions were given of the egg (from the two-cell stage onward), five naupliar, three protozoeal, two mysis, and early postlarval stages. A year-round spawning season is indicated, because eggs were taken at St. Augustine, Fla., from April to August, and at Fort Pierce, Fla., in summer and from December to February. Nauplii were found from April to August, and the remaining stages from May to August, with a few protozoeae being taken also in winter. Pearson found developmental stages of this species more abundant than those of related species in shallow oceanic water; in estuarine water the postlarvae were rare. He attributed this rarity and the comparative scarcity of adults in commercial catches to the burrowing habits of postlarvae and adults, as observed in the laboratory. Somewhat contrary to Pearson's findings, the juvenile stages of this species have been caught commonly in surface plankton tows made with a coarse-mesh net on nightly flood tides in Bogue Sound near Beaufort Inlet, N.C. These collections have been made in summer and fall (mid-June to mid-November) when salinities ranged from 28 to 36 ‰.

Subfamily **Sicyoninae**

Body more or less sculptured and rigid, with prominent, often more or less interrupted dorsal carina. Carapace with or without spine at antennal angle. Lateral section of ocular somite developed into elongated stylet. Basal antennular article lacking enlarged ciliated protuberance (prosartema) on inner proximal margin. No pleurobranchs behind ninth somite (third maxilliped). Fourteenth somite (fifth legs) without gills. Pleopods lacking endopods except in modified form on first and second pleopods of male (modified after Burkenroad, 1934b).

Burkenroad (1934b) pointed out that the subfamily Sicyoninae is an extremely uniform group. Unlike other penaeids, sexual maturity may be attained at a quite small size. "Differences between small and large individuals of any species are slight and chiefly affect rostral length, elevation and distal armature, these features in general becoming respectively shorter, more horizontal, and with more numerous distal teeth as size increases, and the armature of the pleonic [abdominal] pleura, which generally increases in strength and extent with growth." The thelycum, and corresponding male genital sternites, are less varied than among other penaeid groups, and, consequently, are not so serviceable in distinguishing species. The serious student is referred to Burkenroad (1934b, pp. 70-76) for full discussion of these characters.

Genus *Sicyonia* Milne Edwards, 1830

Burkenroad, 1934a, p. 70.—1945, p. 1.—Hall, 1956, p. 87.—Hemming, 1958b, p. 126.

The generic name *Sicyonia* has had a complex nomenclatural history, and was reviewed in detail by Burkenroad (1945) and Hall (1956). The name *Sicyonia* H. Milne Edwards, 1830, has been validated under Plenary Powers of the International Commission on Zoological Nomenclature (Opinion 382; Hemming, 1958b).

KEY TO SPECIES IN THE CAROLINAS

(Modified after Lunz, 1945)

a. Antennal angle not armed with a definite spine; ischium of first leg armed with a spine.
  b. Rostrum (excluding tip) with two dorsal teeth before posterior margin of orbit; carina of carapace with three teeth, first tooth smallest ..... *laevigata* (p. 33).
  bb. Rostrum (excluding tip) with three dorsal teeth; carina of carapace with three evenly spaced, subequal teeth ..... *parri* (p. 34).

aa. Antennal angle armed with definite spine (sometimes blunt); ischium of first leg unarmed.
  b. Three or four teeth on carina of carapace behind orbital margin, three large; carina high; rostrum extending beyond midpoint of cornea, with two dorsal teeth (excluding tip) ..... *brevirostris* (p. 35).
  bb. Two or three teeth on carina of carapace behind orbital margin, two large and behind hepatic spine; rostrum not extending beyond midpoint of cornea, with one or two dorsal teeth (excluding tip) ..... *typica* (p. 36).
  bbb. Two teeth on carina of carapace behind orbital margin, one behind hepatic spine; rostrum with three dorsal teeth (excluding tip).
    c. Fourth abdominal segment with anterior and posterior ends of ventral margin of pleura spined or angular ..... *dorsalis* (p. 37).
    cc. Fourth abdominal segment with posterior end of ventral margin of pleura rounded ..... *stimpsoni* (p. 38).

Sicyonia laevigata Stimpson

Figures 22–23

Sicyonia laevigata Stimpson, 1871b, p. 131.—Hay and Shore, 1918, p. 379, pl. 25, fig. 1.
Eusicyonia laevigata: Burkenroad, 1934a, p. 76, figs. 21, 26, 32 (rev.).—Lunz, 1945, p. 4, fig. 1.

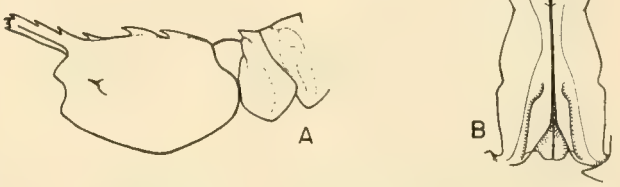

FIGURE 22.—*Sicyonia laevigata* Stimpson. A, carapace and first two abdominal segments in lateral view, approximately × 3; B, petasma of male in ventral view, approximately × 20.5 (A–B after Burkenroad, 1934a).

Recognition characters.—Integument rather firm, finely granulate and more or less sculptured. Rostrum elevated at angle of about 20 degrees, about half as long as carapace; armed dorsally with two teeth not counting tip; terminal portion divided into four teeth; notch between median pair shallower than dorsal and ventral notches; often two short, stout, asymmetrically placed, mobile spines distally above ventral margin. Postrostral carina with three teeth behind orbital margin; anterior one slightly advanced beyond level of hepatic spine and about same size as rostral teeth, often appearing as part of rostral series; posterior two teeth closer together; carina sometimes nearly obliterated anterior to each tooth. Antennal angle unarmed but not rounded. Ocular stylets short.

Abdominal segments marked by tergal carinae deeply notched behind on first to fifth segments. First abdominal segment with carina produced into an elevated anterior tooth; marked laterally by two grooves, a long posteromedian and short anteromedian groove obliterated a short distance ventral to juncture with anterior margin of pleura but with short resumption below juncture. Second and third segments with anterior and short posterior tergal grooves; a short, shallow anteromedian pleural and a posteromedian pleural groove turning sharply anteriad somewhat above middle of lateral surface. Second segment with carina narrowly and deeply cleft above juncture of tergal groove. Fourth and fifth segments with posterior tergal groove, and an anterior groove, obliterated for interval below short dorsal section; reappearing farther ventrad. Sixth segment with a posteromedian pleural, anterior tergal and a longitudinal groove; carina ending in a strong posterior tooth. Ventral pleural margins rounded except for a posterior tooth on fifth and sixth segments.

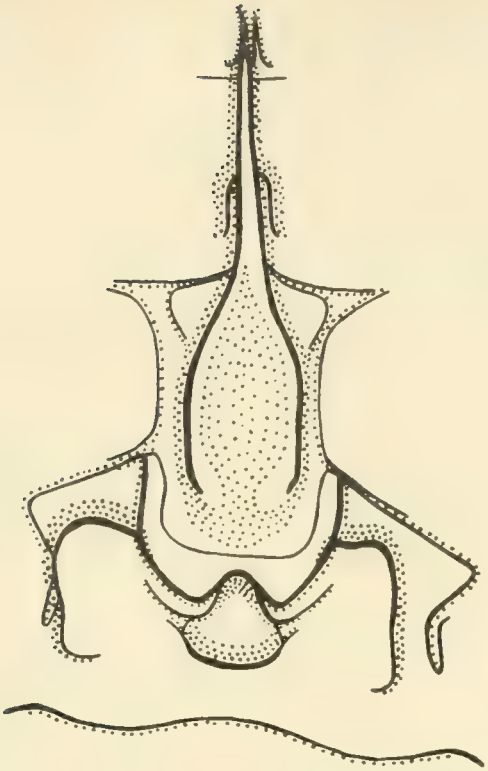

FIGURE 23.—*Sicyonia laevigata* Stimpson. Thelycum of female, × 10.4 (after Burkenroad, 1934a).

Telson ending in a strong point flanked by a pair of shorter blunt spines; sometimes with a pair of mobile lateral spines distal to basal shoulders.

Petasma of male with distolateral projections extending straight distally. Thelycum most conspicuously marked by elongate plate arising on 13th somite (between 4th legs), with slender tip extending to level of 11th somite (2d legs).

Measurements.—Length of body: males, 14 mm.; females, 50 mm.

Variations.—The angle of elevation of the rostrum varies with age. Nearly horizontal among the young, it rises to as much as 35 degrees in older individuals. The usual angle is somewhat in excess of 20 degrees. The number of carinal teeth on the carapace may be reduced to two (Lunz, 1945).

Color.—Yellowish brown; carapace darker than abdomen and sometimes bluish or greenish.

Habitat.—A littoral species fairly common in the Carolinas, especially on shelly bottoms of harbors; shallow water to 49 fathoms.

Type locality.—Charleston, S.C.

Known range.—Cape Hatteras, N.C., to northwest Florida; through West Indies to Colombia; Pacific coast of Panama.

Remarks.—This small species becomes sexually mature at quite a small size (length of 18 mm.).

Sicyonia parri (Burkenroad)

Figure 24

Eusicyonia parri Burkenroad, 1934a, p. 80, fig. 22.—Lunz, 1945, p. 5, fig. 2.

Recognition characters.—Resembling *S. laevigata;* integument rather firm, almost smooth and more or less sculptured. Rostrum elevated at angle of about 15 degrees, armed dorsally with three teeth not counting tip; terminal portion bearing three teeth with rudiment of another between lower teeth. Postrostral carina armed with three large, subequal teeth, anterior one slightly advanced beyond level of hepatic spine.

Abdominal segments marked by tergal carinae notched behind on first to fifth segments. First abdominal segment with carina produced into an elevated anterior tooth, marked laterally with a short anteromedian groove as in *S. laevigata*, but reappearing below obliteration and continuing conspicuously to ventral margin, not connected to posteromedian pleural groove ventrally. Second segment with carina cleft above juncture of tergal grooves. First four segments each with a shallow but perceptible posterior pleural groove. Fourth segment with dorsal and ventral positions of anterior tergal groove separated by narrow area of obliteration.

Petasma of male with distolateral projections curved medially at tips; distoventral lobes constricted abruptly near tip.

Measurements.—Length of body: female, 25 mm.

Habitat.—Shallow water to 14 fathoms.

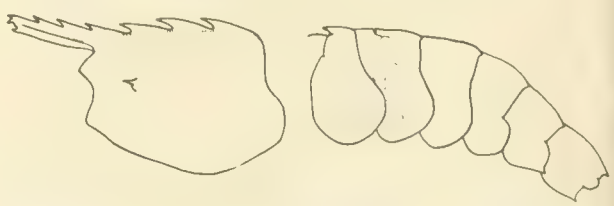

FIGURE 24.—*Sicyonia parri* (Burkenroad). Carapace and abdomen in lateral view, approximately × 3 (after Burkenroad, 1934a).

Type locality.—Crooked Island, Bahamas.

Known range.—Beaufort, N.C.; Florida; West Indies to Curaçao.

Sicyonia brevirostris Stimpson

Figures 25–26

Sicyonia brevirostris Stimpson, 1871b, p. 132.—Hay and Shore, 1918, p. 380, pl. 25, figs. 2, 4.

Eusicyonia brevirostris: Burkenroad, 1934a, p. 84 (rev.).—Lunz, 1945, p. 6, fig. 3.

Recognition characters.—Integument firm, much sculptured, especially abdomen; abdomen with scattered tubercles, and whole body with covering of short, fine hairs. Rostrum short, elevated, slender, narrowing considerably to tip; extending beyond midpoint of cornea; armed dorsally with two (occasionally three) teeth not counting tip; terminal portion divided into two or three teeth with ventral tooth projecting distally farther than dorsal tooth. High postrostral carina with three or four teeth behind orbital margin. Antennal angle armed with a small spine. Hepatic spine well developed. Ocular stylets long.

Abdominal segments marked by prominent tergal carinae deeply notched behind on first to fifth segments. First abdominal segment with carina produced into an elevated anterior tooth; marked laterally by four grooves, an anteromedian and posteromedian pleural, a posterior pleural and posterior tergal. Second and third segments grooved with two tergals, two median pleurals extending far dorsad, and a posterior pleural. Fourth segment grooved with two tergals and one pleural; fifth with two tergals. Sixth segment with a posteromedian pleural, anterior tergal, and a longitudinal groove. Fifth and sixth segments each with carinal tooth directed posteriorly. Pleura of first four segments armed with an anterior ventral angle; angle produced into blunt, outward pointing spine on third and fourth, sometimes also on second segment. Last three segments armed with posterior ventral tooth. Telson ending in a strong point flanked by a shorter pair of subterminal, often obsolescent, spines.

FIGURE 25.—*Sicyonia brevirostris* Stimpson. Carapace and first two abdominal segments in lateral view, 5 mm. indicated (after Lunz, 1945).

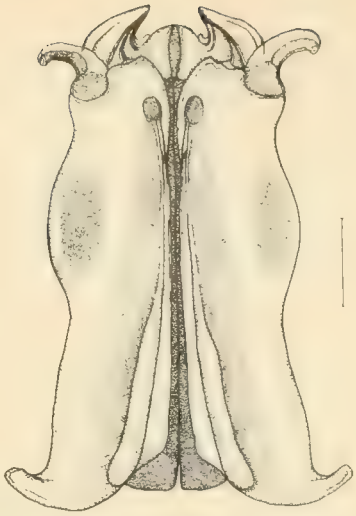

FIGURE 26.—*Sicyonia brevirostris* Stimpson. Petasma of adult male, ventral view, 1 mm. indicated.

Petasma of male with distolateral lobes curved medially, distoventral lobes curved laterally.

Measurements.—Length of body: males and females 153 mm.

Variations.—This species exhibits considerable variation in degree of elevation of the rostrum (5–45 degrees). The rostral length also varies, and length and angle of elevation tend to decrease with increasing age, but this tendency is highly irregular.

Considerable variation in placement of teeth on the carapace occurs. The anterior tooth of the dorsal carina may be located behind the orbital margin and appear as part of the carapace series, in which case there are four teeth on the carapace and two on the rostrum (exclusive of tip); or, this tooth may be located anterior to the orbital margin and appear as part of the rostral series, in which case there are three teeth on the rostrum and three on the carapace.

Color.—Ground color off white to light pink, pubescence grayish to grayish yellow; dorsal carina barred with white; appendages reddish

purple, thoracic appendages barred with white; ventral side of abdomen and uropods reddish, sternal ridges white with purple tipped median spines. Burkenroad (1939) gave a somewhat different and more detailed color description.

Habitat.—Common in offshore littoral of the Carolinas; on white shell sand on Campeche Banks; shallow water to over 100 fathoms in Carolinas (Broad, 1950), rarely to 180 fathoms.

Type locality.—Cuba.

Known range.—Off Norfolk, Va., through Bahamas and Gulf of Mexico to Yucatan, Mexico; Pacific coast of southern Mexico.

Remarks.—This large sicyonine shrimp is fairly common in North Carolina and has had a limited commercial usage. Formerly thought to be rare in South Carolina (Lunz, 1945), it is now found to be widely distributed out to the 50-fathom curve (Lunz, 1957). Eldred (1959) reported few *S. brevirostris* in the Tortugas controlled area off Florida. Hildebrand (1954) found the species to be fairly abundant on the Campeche fishing grounds where the bottom is white shell sand. On the Texas brown shrimp grounds and Campeche Banks, the species is rare in depths of 15–25 fathoms where *S. dorsalis* predominates on mud bottom. In deeper water and on mud bottom, 31–45 fathoms, it is more abundant. It is also common in shallow water at 6–10 fathoms. Hildebrand suggested a distribution in two zones separated by an intermediate zone where *S. dorsalis* predominates, or possibly the deeper zone of *S. brevirostris* over mud represents strays. On Campeche Banks, *S. brevirostris*, *dorsalis*, and *typica* have been taken together.

Lunz (1957) reported natural history notes on *S. brevirostris* in South Carolina based on 169 successful 30-minute hauls with a 20-foot experimental trawl. He found the species most abundant in depths of 35–40 fathoms. Catches at night were larger than those made in daytime. Though available throughout the year, largest catches were made in December. Meager data on maturity of gonads indicated spring and fall spawning seasons.

Sicyonia typica (Boeck)

Figure 27

Sicyonia carinata Milne Edwards, 1830, p. 344, pl. 9, fig. 9.—Bate, 1888, p. 294, pl. 43, figs. 2–3.

Synhimanntites typica Boeck, 1864, p. 189.—Danielssen and Boeck, 1872, p. 192, figs. 1–14.—Sars, 1883, pp. 8, 49.

Sicyonia edwardsii Miers, 1881, p. 367.—Milne Edwards and Bouvier, 1909, p. 251, pl. 8, figs. 1–3 (not fig. 4) (rev.).—Hay and Shore, 1918, p. 380. Schmitt, 1935a, p. 133 (not fig. 6).—Lunz, 1945, p. 7, fig. 4.

Sicyonia typica: Burkenroad, 1945, p. 2 (rev.).—Holthuis, 1959, p. 77.

Recognition characters.—Integument rather firm, more or less sculptured and covered with a short, thick pubescence more evident dorsally than ventrally, especially on abdomen. Rostrum extending halfway along eye, directed obliquely upward, armed dorsally with one or two small teeth not counting tip. Postrostral carina with two or three teeth, last two placed behind level of hepatic spine (third tooth, if present, may look like part of rostral series). Antennal angle armed with a short, often blunt, tooth.

Abdominal segments marked by tergal carinae deeply notched behind on first to fifth segments; first segment with carina produced into an elevated anterior tooth; fifth segment with carina ending posteriorly in a low tooth; sixth segment with carina produced into a posteriorly directed tooth. Pleura of first four segments with a ventrally directed acute tooth on distal margin (character apparent only in large adults). Fifth and sixth segments with tooth at posterolateral corner of pleura, that of fifth often small and rectangular. Abdominal grooves deep and well defined. First segment with posteromedian and anteromedian grooves connected ventrally. Second segment with anterior and posterior tergal grooves connected dorsally; anterior and median pleural grooves connected dorsally and ventrally; a thin and more or less interrupted posterior pleural groove connected with posterior tergal. Telson usually lacking subterminal spines.

Measurements.—Length of body: 74 mm.

Variations.—Position of the posterior rostral tooth is variable. In some individuals this tooth

FIGURE 27.—*Sicyonia typica* (Boeck). Carapace and first abdominal segment in lateral view, 1 mm. indicated (after Lunz, 1945).

is located behind the orbital margin, thus appearing as one of the carinal series on the carapace (Lunz, 1945).

Color.—Blue spots in tail prominent in life; bright red blotch surrounding rostrum (note by W. L. Schmitt in U.S. National Museum records).

Habitat.—Between tide marks to 37 fathoms.

Type locality.—Molde Fjord, west coast of Norway [erroneous locality, evidently incorrectly labeled].

Known range.—Beaufort, N.C.; east and west Florida; Gulf of Campeche; Cuba through West Indies to Rio de Janeiro, Brazil.

Remarks.—Hildebrand (1954) stated that this species is taken in commercial quantities in the Gulf of Batabano off southwest Cuba, and occurs in commercial but unexploited quantities in parts of the Gulf of Campeche.

There remains some doubt that this species occurs in North Carolina, though Lunz (1945) stated that it does. If so, it is not common.

Sicyonia dorsalis Kingsley

Figure 28

Sicyonia dorsalis Kingsley, 1878b, p. 97.—Hay and Shore, 1918, p. 380, pl. 25, fig. 3.
Eusicyonia dorsalis: Burkenroad, 1934b, p. 121, figs. 13, 14 (rev.).—Lunz, 1945, p. 8, fig. 5.

Recognition characters.—Body small, slightly compressed. Carapace minutely punctate, less deep and inflated than *S. stimpsoni.* Rostrum extending horizontally or decurved variable distance beyond eye; ridge on lateral surface sloping upward to near dorsal margin; armed dorsally with three teeth not counting tip, posterior tooth in front of orbital margin and placed variable distance from anterior carinal tooth of carapace; tip appearing bifurcate, dorsal tooth greatly enlarged, ventral tooth reduced to blunt angle.

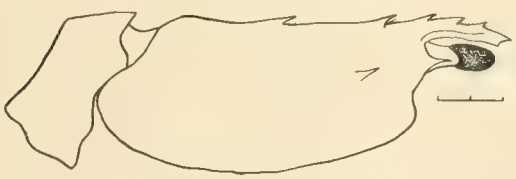

FIGURE 28.—*Sicyonia dorsalis* Kingsley. Carapace and first abdominal segment in lateral view, 2 mm. indicated (after Lunz, 1945).

Postrostral carina with two teeth, anterior tooth before level of hepatic spine, posterior tooth near midpoint. Antennal angle armed with a spine.

Abdominal segments with conspicuous tergal carinae; margins of notches at posterior ends of carinae on segments three to five sometimes produced into long slender spines. First abdominal segment with tergal carina produced into an elevated anterior tooth; anteroventral margin of pleura concave (or at least straight in young) and with an anterior angle in addition to one in middle of ventral edge, posterior angle sometimes produced into a dentiform projection. Second abdominal segment with tergal and pleural grooves connected as an uninterrupted groove extending full depth of segment. Ventral margins of pleura in segments three and four each with both anterior and posterior angle, anterior sometimes sharp, posterior sometimes armed with strong curved spine. Fifth segment with posterior spine only. Tergal carina of sixth segment extended into a posterior spine.

Petasma of male with distoventral lobe forked.

Measurements.—Length of body: male 63 mm.; female 71 mm.

Variations.—Angles and spines on the pleura become better defined with increasing age.

Habitat.—Common on mud bottom (Hildebrand, 1954), or mud and shells (Holthuis, 1959); from 3 to 88 fathoms, rarely to 230 fathoms.

Type locality.—Fort Jefferson, Dry Tortugas, Fla.

Known range.—Cape Hatteras, N.C., to Texas; Colombia to French Guiana.

Remarks.—Hildebrand (1954, 1955) listed this species as third in abundance on the brown shrimp grounds in Texas but less common on Campeche Banks. It is most common in 15–25 fathoms but ranges shoreward to depths of 6.5 fathoms, and small specimens were occasionally taken in the mouths of bays. Eldred (1959) listed this species as the most common among *Sicyonia* species taken in the Tortugas controlled area in Florida.

Adults of this species fouled with the barnacle, *Balanus amphitrite niveus* Darwin, and *Polydora* sp., were reported from the Gulf of Mexico off Marquesas Key by Eldred (1962). Such specimens, ranging in size from 58 to 70 mm. total length, were judged to be near maximum size for the species.

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Sicyonia stimpsoni Bouvier

Figure 29

Sicyonia stimpsoni Bouvier, 1905, p. 748.—Holthuis, 1959, p. 75.

Sicyonia dorsalis: Milne Edwards and Bouvier, 1909, p. 253, text-figs. 86–88, pl. 8, figs. 4–13.

Eusicyonia stimpsoni: Burkenroad, 1934b, p. 121 (notes).—1939, p. 57.

Eusicyonia edwardsii: Schmitt, 1935a, p. 133, fig. 6.

Recognition characters.—Rostrum usually elevated at considerable angle, extending variable distance beyond eye; with three dorsal teeth not counting tip, posterior tooth in front of orbital margin separated by a variable distance from anterior carinal tooth of carapace; tip often appearing bifurcate but a third ventral tooth present behind or below level of anterior cleft; a slight ridge on lateral surface running parallel with ventral margin. Postrostral carina with two teeth, anterior tooth before level of hepatic spine, posterior tooth behind midpoint; sometimes rudiment of a third tooth appearing as a minute crest-like swelling with truncated anterior edge a little in front of posterior tooth. Antennal angle armed with a spine.

Abdominal segments with conspicuous tergal carinae. First segment with carina produced into an elevated anterior tooth. Margins of dorsal notches at posterior ends of segments three to five produced as short angular projections. A tooth at posterior end of fourth to sixth segments. Segments one to four with a ventral spine on pleura; segments five and six with spine at posteroventral corner. Second abdominal segment with pleural groove curving forward midlaterally, not connected to short tergal groove curving downward and backward.

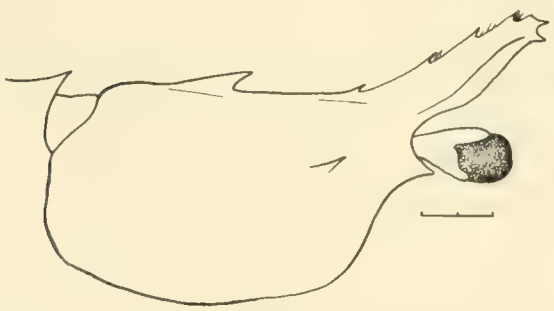

FIGURE 29.—*Sicyonia stimpsoni* Bouvier. Carapace and portion of first abdominal segment in lateral view, 2 mm. indicated (after Lunz, 1945).

Petasma of male with distoventral lobe not forked.

Measurements.—Length of body: male, 44 mm.; female, 60 mm.

Variations.—Pleural spines may be absent in young individuals.

Color.—Branchial region of carapace with orange, or brownish and yellowish-white ring in posterior half (Holthuis, 1959). North Carolina specimens show a purple spot with surrounding vermilion ring in this region.

Habitat.—Found on predominantly mud and shell bottom in Surinam (Holthuis, 1959); shallow water to 230 fathoms.

Type locality.—Off Barbados, British West Indies, lat. 13°03′05″ N. long. 59°36′18″ W., depth 103 fathoms.

Known range.—Cape Hatteras, N.C., to Campeche Gulf; West Indies to French Guiana.

Remarks.—Among species of *Sicyonia* occurring in the Carolinas, the only detailed description of development is that given by Pearson (1939) for this species. Eggs attributed to this species were taken in inlets, and larval development (reconstructed from plankton) proceeded through five naupliar, three protozoeal, and two mysis stages. Eggs were taken abundantly at St. Augustine Inlet, Fla., in plankton, from March 30 to August 8; they were taken in lesser abundance from January to March, and August to September at Fort Pierce, Fla., and off Stono Inlet, S.C., in September. Naupliar and protozoeal stages were found from April to August, and mysis stages were found in January and August–September. Thus, the breeding season along that stretch of coast lasts at least from January to September.

Holthuis (1959) noted that males in Surinam material outnumbered females about 3 to 1.

Family **Sergestidae**

Penaeidea with last two pairs of legs reduced in size or lost; gills few or lost.

KEY TO SUBFAMILIES AND SPECIES IN THE CAROLINAS

a. Head not greatly elongated; gills present
Sergestinae; *Acetes americanus carolinae* (p. 39).

aa. Head greatly elongated; gills absent
Luciferinae; *Lucifer faxoni* (p. 40).

Subfamily **Sergestinae**

Carapace moderately compressed. Inferior antennular flagella present; with prehensile organ in male. Second and third pair of legs, at least, terminated by a pincer. Gills present. Sixth abdominal segment and telson without sexual differences; without protuberances or ventral processes in males. Petasma with a short base. No protuberance on peduncle of first pleopod (after Hansen, 1922).

Genus ***Acetes*** Milne Edwards, 1830

Burkenroad, 1934a, p. 99.—1934b, p. 126.

Acetes americanus carolinae Hansen

Figures 30–31

Acetes americanus Ortmann, 1893, p. 39, pl. 2, fig. 2.
Acetes carolinae Hansen, 1933, p. 31, figs. 1–8.
Acetes americanus carolinae: Holthuis, 1959, p. 49, fig. 1, a–c (rev.).

Recognition characters.—Body small. Integument thin, smooth, polished. Carapace with rostrum elevated, short; a single tooth behind acute tip. A prominent spine on rounded ridge behind eye; hepatic spine small. Eyes prominent, stalk conical, cornea large. Antennules with peduncle long, third article more than twice length of second article, lower flagellum much shorter and more slender than upper, upper hairy ventrally near base; in males, curved lower flagellum forming clasping organ, basal four annulations thicker than distal annuli, third and fourth armed dorsally with a short row of spines, distal one strongest. Antennal scale reaching end of second article of antennular peduncle in males, beyond end of second article in females.

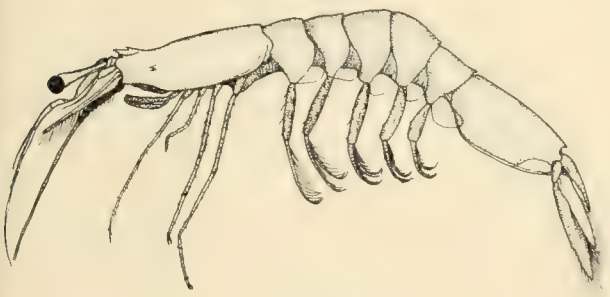

FIGURE 30.—*Acetes americanus carolinae* Hansen. Female in lateral view, × 4.8.

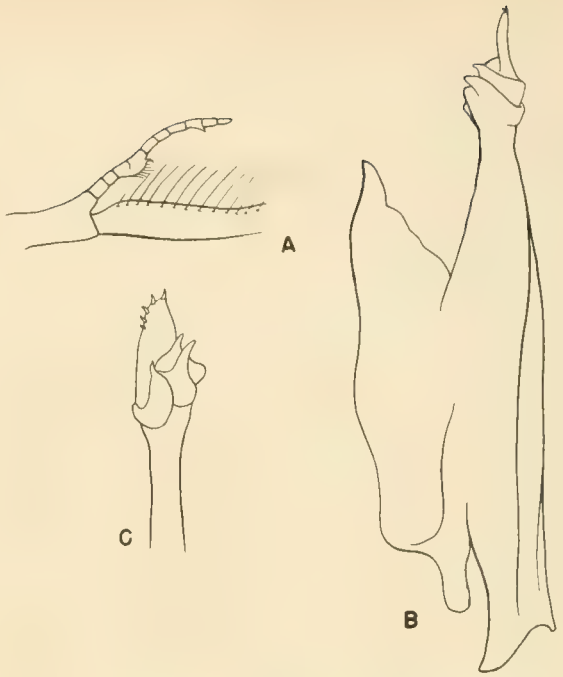

FIGURE 31.—*Acetes americanus carolinae* Hansen. A, clasping organ on antennule of male × 50; B, petasma of male, right side in posterior view × 90; C, tip of petasma, anterior view of right side × 90.

Sixth segment of abdomen with convex ventral margin bifurcated caudally. Exopod of uropod about 4.5 times longer than broad; proximal three-fifths of outer margin smooth, ending in a minute tooth, remainder of margin hairy.

Petasma of male with membranous, triangular-tipped external portion exceeded by slender median part; median portion ending in complicated capitulum, a distomedian crooked lobe tipped with four thick, short spines, and three other shorter lateral lobes each produced into an acute point. Lobes behind base of last pair of legs greatly enlarged in males forming genital coxae broader than long. Coxae of third legs in females with posteromedian corner produced into a protuberance; sternite immediately behind third legs bearing two curved projections forming a U-shaped thelycum.

Measurements.—Length of body: 15 to 26 mm.

Variations.—Holthuis (1948, 1959) followed Burkenroad (1934a) in considering the known species of *Acetes* from the western Atlantic with one tooth behind the tip of the rostrum to be all

A. americanus. Burkenroad recognized four subspecies: *A. americanus americanus* Ortmann, Brazil; *A. a. limonensis* Burkenroad, Panama; *A. a. louisianensis* Burkenroad, Louisiana; *A. a. carolinae* Hansen, North Carolina. Holthuis considered these to be clinal variants, with the northern and southern representatives differing most widely from each other. Females of the four doubtfully valid subspecies differ in depth of the concavity in the middle of the posterior segment of the genital sternite. This structure is deeper than broad in Carolinian specimens, but becomes shallower in progressively more southern forms. Holthuis suggested that the extreme northern and southern forms might deserve to retain subspecific rank.

Color.—Nearly transparent with faint red flecks.

Habitat.—Littoral oceanic and estuarine waters to 23 fathoms.

Type locality.—Typical form, mouth of Pará (=Tocantins) River, [State of Pará], Brazil. Northern form, off Beaufort Inlet, N.C.

Known range.—Cape Lookout, N.C., to mouth of Pará River, Brazil.

Remarks.—Burkenroad (1934b) found larval stages of this *Acetes* at the surface of the outer littoral of Louisiana in spring. He described the spermatophore as gourd-shaped, much as the spermatophore of *Lucifer*, and gave other structural details of the reproductive system.

In Bogue Sound, near Beaufort Inlet, N.C., specimens have been taken in every month of the year in a large plankton net fished from a pier at the surface on flood tides at night. Gutsell (*in* Hansen, 1933) reported that this species can sometimes be taken near Beaufort Inlet, N.C., "in gallons at a time," especially in late summer and early fall.

Subfamily **Luciferinae**

Carapace extremely compressed. Antennules without inferior flagella in both sexes. Third pair of legs only terminated by a pincer. Gills absent. Sixth abdominal segment of male with two ventral processes, second far behind first. Telson of male with a strong protuberance on internal face. Petasma sessile, proximal part fixed like a large disc on peduncle of first pleopod; each peduncle, near disc, possessing a protuberance with distal spines (after Hansen, 1922; Burkenroad, 1934b).

Genus ***Lucifer*** Thompson, 1829

Hansen, 1919, p. 48.

Lucifer faxoni Borradaile

Figure 32

Lucifer faxoni Borradaile, 1915, p. 227.—Hay and Shore, 1918, p. 381, text-fig. 4, pl. 26, fig. 10.—Holthuis, 1959, p. 52 (rev.).

Recognition characters.—Body small, thin; integument smooth, thin, transparent. Anterior portion of cephalothorax cylindrical, greatly lengthened (about 1.5–2.5 times longer than posterior portion), bearing eyes, antennules, and antennae far in front of mouth parts and legs. Rostrum small, a spine on each side behind eye and at anterolateral corner. Posterior portion of cephalothorax with spine on each side in front. Eyes large, prominent, on stout conical stalks about one-fourth to one-third length of anterior part of cephalothorax. Peduncles and flagella of antennules long, slender. Peduncle of antennae about half as long as first article of antennular peduncle; flagellum longer than that of antennule; antennal scale almost linear, fringed on inner margin with long hairs.

Third maxilliped long, pediform. Three pairs of legs; first pair short; last two pairs of equal length extending almost to end of cephalothorax.

Abdomen much compressed; segments deepest and produced into spiniform angle where pleopods originate. Sixth segment as long as preceding two segments, posterolateral angles spiniform near

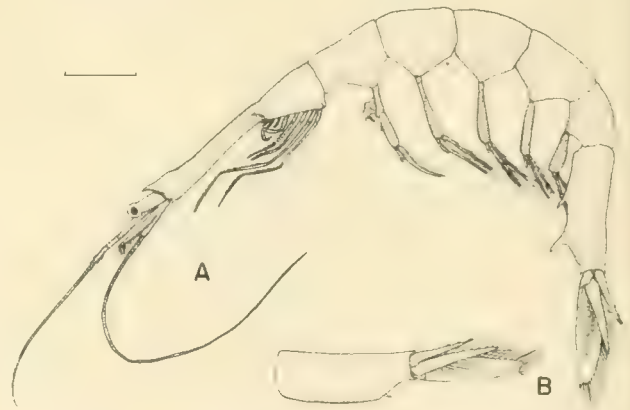

FIGURE 32.—*Lucifer faxoni* Borradaile. A, male in lateral view; B, sixth abdominal segment and tail fan of female in lateral view; 1 mm. indicated.

base of uropods; a small median spine above base of telson; male with two strong ventral spines, posterior spine curved and about twice length of anterior spine. Telson slender, about half length of uropods; truncate distally with a strong spine at each corner; two pairs of intermediate spines on distal border, and two pairs of lateral spines about equidistant; males with a prominent ventral projection on distal half. Outer ramus of uropod longer and broader than inner.

Petasma of male membranous, folded, foliaceous; ventral process needlelike, curved, tapering to acute end directed ventrolaterally.

Measurements.—Length of body: 10–12 mm.

Color.—Almost perfectly transparent in life.

Habitat.—Oceanic and estuarine waters from surface to 50 fathoms.

Type locality.—Off Chesapeake Bay.

Known range.—Off Nova Scotia along coast of United States to Louisiana; through West Indies and along coast of South America to off Rio de Janeiro, Brazil; Bermuda and mid-Atlantic (lat. 42°50′26″ N. long. 41°48′ W., lat. 41°39′34″ N. long. 39°21′ W., and lat. 4°30′ N. long. 28°20′ W.); Rea Sea; Malay Archipelago; Marshall Islands; Hawaiian Islands; Fanning Island (Holthuis, 1959).

Remarks.—This interesting little shrimp is abundant near Beaufort Inlet, N.C., throughout most of the year (collected from February through October), and often occurs in swarms outside the harbor.

Brooks (1882) worked out the larval development of a species of *Lucifer* in the Beaufort, N.C., area, and from his figures and present knowledge of distribution, it is almost certain that he was dealing with *L. faxoni.* Brooks found egg-bearing females only in April, but found larvae as late as September. Since then, egg-bearing females have been found through the summer into October in Bogue Sound near Morehead City, N.C. Brooks illustrated the egg, a number of larval stages (two nauplius, three protozoea, one zoea, one schizopod, one mastigopus, and one lucifer), and a final adult stage in males.

As various authors have pointed out, Brooks mistakenly thought that the species was primarily estuarine, the adults leaving the marshes on ebb tides to spawn in the ocean, because he found the species most concentrated in the estuary near Beaufort on ebb tides. He failed to find specimens on flood tide. The species can be found in estuaries on both flood and ebb tide, but its primary home is the ocean.

Burkenroad (1934b) reported a female with large ova from the outer littoral of Louisiana. He gave a detailed account of the reproductive systems of males and females showing that they are fully bilateral and not asymmetrical as stated by Brooks (1882), Bate (1888), and Hansen (1922). The males, however, carry but one spermatophore at a time, possibly because the body is so strongly compressed.

Section **Caridea**

Pleura of second abdominal segment overlapping those of first and third segments. Third legs never with chelae. Gills phyllobranchiate (Holthuis, 1955).

Family **Pasiphaeidae**

Rostrum small or obsolete. Mandibular palp absent, one or two jointed. Legs with exopods; first two pairs of legs chelate, chelae slender, cutting edges pectinate; third, fourth, and fifth legs smaller than chelipeds, fourth generally smallest (Rathbun, 1901; Holthuis, 1955).

Genus ***Leptochela*** Stimpson, 1860

Stimpson, 1860, p. 111.—Hemming, 1958b, p. 157.

Leptochela serratorbita Bate

Figures 33–34

Leptochela serratorbita Bate, 1888, p. 859, pl. 139, fig. 1.—Rathbun, 1901, p. 127.—Schmitt, 1935a, p. 134.

Recognition characters.—Carapace smooth, anterior half with low carina. Rostrum nearly horizontal, unarmed, about as long as eyestalks. Upper portion of orbits finely serrated or spinulose.

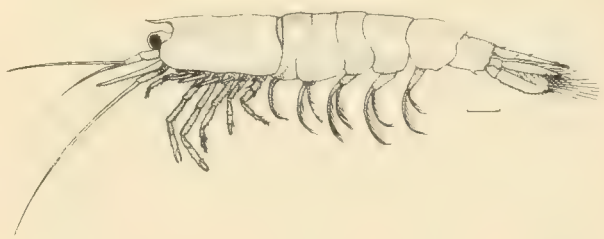

FIGURE 33.—*Leptochela serratorbita* Bate. Animal in lateral view, 1 mm. indicated.

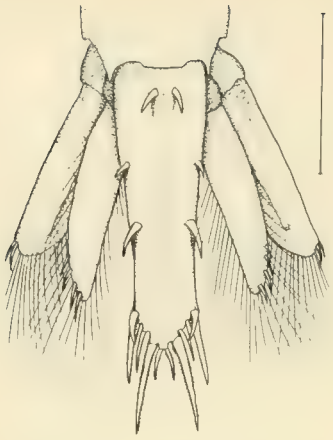

FIGURE 34.—*Leptochela serratorbita* Bate. Uropods and telson in dorsal view, 1 mm. indicated.

Antennal spine small or absent. Antennular peduncle reaching beyond middle of antennal scale.

First two pairs of legs chelate; fingers a little longer than palm, cutting edges pectinate.

Abdomen with fourth and fifth segments broadly carinate; sixth segment with an anterior middorsal tubercle, a posterior spine either side of middle and a prominent spine preceding each posterolateral angle. Telson with an anterior submedian pair of spines and three pairs of lateral marginal spines, anterior lateral spines at anterior fourth, second at middle, third near posterior extremity; tip with three pairs of unequal spines and two pairs of strong setae, all more or less fimbriated. Exopod of uropod with a row of spines along ventrolateral border, a long curved spine at tip; endopods spiny near tip.

Measurements.—Length of body: 21 mm.

Habitat.—Known only from coastal and occasionally estuarine waters, from surface to 23 fathoms (perhaps to 33 fathoms).

Type locality.—St. Thomas, shallow water.

Known range.—Near Beaufort Inlet, N.C.; Charleston Harbor, S.C.; Key West, Fla.; Puerto Rico, and Virgin Islands.

Remarks.—This small shrimp has been taken in May, July, October, and November in surface plankton tows in Bogue Sound, near Beaufort Inlet, N.C., on flood tides at night. The specimen taken in May was ovigerous. Lunz (1939) collected a specimen in July in South Carolina.

Family **Palaemonidae**

Caridea having first two pairs of legs chelate, second pair usually larger than first, carpus of second pair not subdivided. Rostrum usually armed with teeth and not movable. Mandibles usually with an incisor process (Holthuis, 1951a).

KEY TO SUBFAMILIES IN THE CAROLINAS

a. Posterior margin of telson with three pairs of spines ..... Pontoniinae (p. 42).

aa. Posterior margin of telson with two pairs of spines and two or more setae ..... Palaemoninae (p. 50).

Subfamily **Pontoniinae**

Upper antennular flagellum with both rami fused in basal part. Appendix masculina generally present on second pleopod of male; appendix interna on second pleopod of female. Pleurobranch absent from third maxilliped. Posterior margin of telson with three pairs of spines (Holthuis, 1951a).

KEY TO GENERA AND SPECIES IN THE CAROLINAS

(Holthuis, 1951a, modified)

a. All maxillipeds with well-developed exopods.

b. Hepatic spine present ..... *Periclimenes* (p. 42).

c. Antennal spine absent; dactyls of last three legs bifurcate ..... *P. longicaudatus* (p. 42).

cc. Antennal spine present; dactyls of last three legs simple ..... *P. americanus* (p. 43).

bb. Hepatic spine absent.

c. Rostrum compressed, with distinct teeth ..... *Periclimenaeus* (p. 45).

d. Antennal scale with no terminal tooth ..... *P. schmitti* (p. 45).

dd. Antennal scale with terminal tooth ..... *P. wilsoni* (p. 46).

cc. Rostrum depressed, with at most two small teeth near tip ..... *Pontonia* (p. 47).

d. Dorsal spines of telson small and rather inconspicuous ..... *P. domestica* (p. 47).

dd. Dorsal spines of telson well developed ..... *P. margarita* (p. 48).

aa. Second and third maxillipeds without exopods ..... *Neopontonides beaufortensis* (p. 49).

Genus ***Periclimenes*** Costa, 1844

Subgenus ***Periclimenes*** Costa, 1844

Holthuis, 1951a, p. 23, 26.—Hemming, 1958b, p. 159.

Periclimenes (Periclimenes) longicaudatus (Stimpson)

Figure 35

Urocaris longicaudata Stimpson, 1860, p. 39.—Hay and Shore, 1918, p. 394, pl. 27, fig. 7.

Periclimenes (Periclimenes) longicaudatus: Holthuis, 1951a, p. 26, pl. 6, figs. a–m; pl. 8, fig. m (rev.).

Recognition characters.—Rostrum straight, short, reaching to end of second or third article

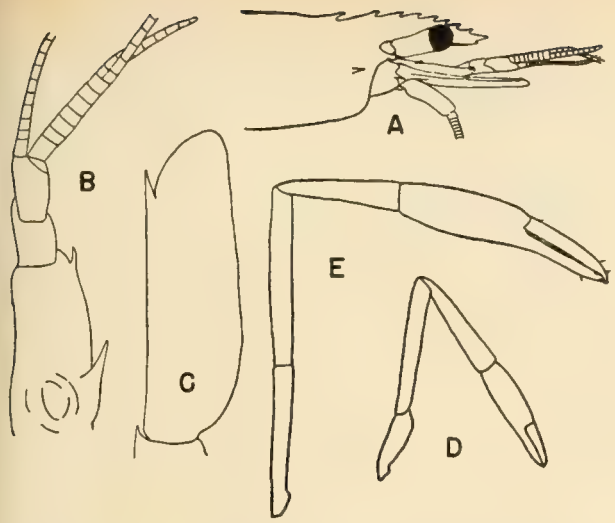

FIGURE 35.—*Periclimenes* (*Periclimenes*) *longicaudatus* (Stimpson). A, anterior part of body in lateral view, × 5; B, antennule, × 11.5; C, antennal scale, × 11.5; D, first leg, × 13.0; E, second leg, × 13.0 (after Holthuis, 1951a).

of antennular peduncle; upper margin raised into a high arcuate crest with seven to nine teeth, first two teeth behind orbit more widely spaced than distal teeth; lower margin with one or two small spines near tip. Carapace with lower angle of orbit produced into a lobe constricted at base; supraorbital and antennal spines absent; anterolateral angle rounded. Eyes well developed and elongate. Stylocerite well developed but not reaching to middle of basal antennular article; basal antennular article convex and ending in a strong spine; upper antennular flagellum with two rami fused for four to eight joints. Antennal scale with outer margin slightly concave, ending in a strong tooth exceeded distally by lamella; antennal peduncle reaching almost to middle of scale, with distinct outer spine near base of scale. All maxillipeds with well-developed exopods.

First legs slender, reaching almost to end of antennal scale; second legs equal in size and shape, stronger and longer than first legs.

Abdomen smooth; all pleura rounded. Third abdominal segment somewhat produced in middle of posterior margin. Sixth abdominal segment twice length of fifth and longer than telson. Telson with two pairs of dorsal spines both lying behind middle; posterior margin with three pairs of spinules.

Measurements.—Length of body: male, 17 mm.; ovigerous females, 15 to 22 mm.

Color.—Body transparent in life.

Habitat.—This species is found in abundance on submerged vegetation along with *Hippolyte* and *Tozeuma*, on *Leptogorgia*, algae and *Sargassum*, or from sponges (Schmitt, 1924b); however, it is hard to detect because of its almost perfect transparency. Surface to 6 fathoms, rarely to 15 fathoms.

Type locality.—Coast of Carolina.

Known range.—Hatteras, N.C., to southwestern Florida; West Indies to State of Paraíba, Brazil. There are doubtful records from the Indian Ocean and deeper waters of the Gulf of Mexico (Holthuis, 1951a).

Remarks.—This species is abundant in the Beaufort, N.C., area, and has been collected there throughout the year. Ovigerous females have been found from May through October. They occur in Cuba in January and March (Schmitt, 1924b) and in Texas in May. Pearse and Williams (1951) found the form on reefs off the North Carolina coast along with an unidentified *Periclimenes*. Last larval, postlarval, and early juvenile stages doubtfully assigned to this species have been described by Gurney and Lebour (1941) from Bermuda.

Subgenus ***Harpilius*** Dana, 1852

Holthuis, 1951a, p. 23.

Periclimenes* (*Harpilius*) *americanus (Kingsley)

Figure 36

Anchistia americana Kingsley, 1878b, p. 96.
Periclimenes (*Harpilius*) *americanus:* Holthuis, 1951a, p. 60, pl. 18, figs. a–j; pl. 19, figs. a–e (rev.).

Recognition characters.—Rostrum rather high and straight; tip directed upward, reaching about to end of antennular peduncle; upper margin nearly straight, with 7–10 teeth, first two behind orbit and considerably separated; lower margin with 2, sometimes 3 teeth but with an unarmed stretch before tip. Carapace with only antennal and hepatic spines; lower orbital angle acute; postorbital ridge paralleling orbit; anterolateral angle broadly rounded. Eyes well developed; cornea globular, two dark-colored bands visible on cornea in fresh material; an ocellus present. Stylocerite rather strong, sharply pointed, almost reaching middle of basal antennular article; outer

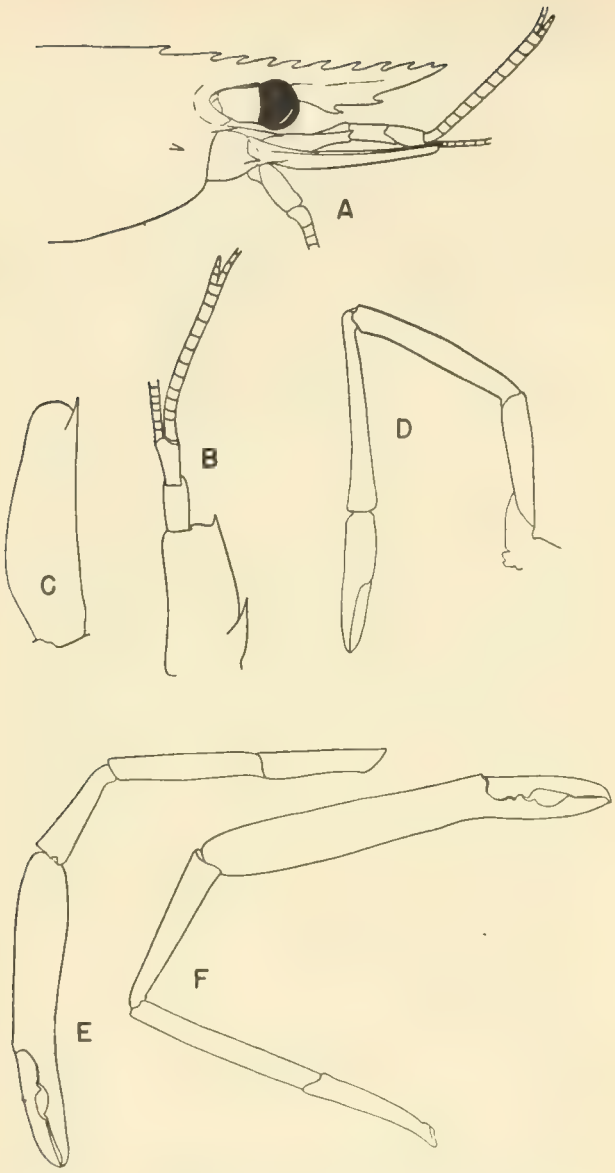

FIGURE 36.—*Periclimenes* (*Harpilius*) *americanus* (Kingsley). A, anterior part of body in lateral view, × 8.5; B, antennule, × 11; C, antennal scale, × 11; D, first leg, × 11; E, F, second leg (different specimens), × 7.5 (after Holthuis, 1951a).

margin of basal antennular article convex, ending in well-developed anterolateral tooth; second and third articles elongate, second slightly shorter than third; upper antennular flagellum with 2 rami fused for 8–12 joints (often 6 in younger specimens), free portion of shorter ramus with 3 or 4 joints, length less than one-fourth that of fused part. Antennal scale slightly exceeding antennular peduncle, outer margin straight or slightly concave and ending in a strong tooth slightly exceeding distally narrowed lamella; scale with a distinct spine near base; antennal peduncle not reaching to middle of scale. All maxillipeds with well-developed exopods.

First legs slender; chela and sometimes a small portion of carpus extending beyond antennal scale; fingers smooth, as long as palm. Second legs equal in size and shape, very strong and longer than first; adult males with fingers less than half as long as palm, three or four teeth on cutting edges leaving gape at midlength when closed; second legs shorter and fingers not agape in juveniles and adult females.

Abdomen with pleura of first four segments rounded, of fifth ending in a small tooth; median posterior margin of third only slightly produced posteriorly. Sixth segment about 1.5 times as long as fifth and about three-fourths length of telson. Telson with two dorsal pairs of spines at one-third and two-thirds length; posterior margin with three pairs of spines, intermediate pair less than twice length of inner spines.

Measurements.—Length of body: male 22 mm.; ovigerous females, 13 to 20 mm.

Variations.—The carpus of the second pair of legs varies in length as do the dactyls of the last three pairs of legs.

Color.—Ground color translucent grayish white; carapace with three oblique orange-brown lateral lines and a pair of dorsal lines running back from base of rostrum; each abdominal segment crossed by a narrow brown band and a row of small dark spots on posterior margin; tail fan with two larger lateral and median spots and an orange-brown tip (Verrill, 1922).

Habitat.—This species lives in coastal waters, preferring sandy or rocky bottom, often between algae or coral. Verrill (1922) found large schools near the surface in Bermuda, and Gurney (1943a) found it to swim singly or in small numbers at the surface at night in certain periods of the lunar cycle (see Holthuis, 1951a). Shallow water to 40 fathoms.

Type locality.—Key West, Fla.

Known range.—Beaufort, N.C.; Jupiter Inlet, Fla., to west coast of Florida off Hernando County; off Cape Catoche, Yucatan, Mexico; through West Indies to Aruba; Bermuda.

Remarks.—Gurney (1943a) listed this species as one of the commonest decapod crustaceans in the littoral region of Bermuda. Females outnumbered males two to one; however, ovigerous females were never collected there. From plankton, Gurney (1936c, 1943a) described the first and fifth larval, and the first postlarval stages, and gave remarks on allometric growth of the second legs. These legs are stronger and longer in males than in females, with fingers agape in old males. The center of greatest growth is in the palm.

Ovigerous females have been found from January to May and from September to November in Florida, the West Indies, and South America.

Holthuis (1951a) listed *P. americanus* as common in North Carolina, but it has been taken only once (August 5, 1958) in surface plankton tows in Bogue Sound that have produced hundreds of *P. longicaudatus*.

Genus ***Periclimenaeus*** Borradaile, 1915

Holthuis, 1951a, p. 76.—Hemming, 1958b, p. 159.

Periclimenaeus schmitti Holthuis

Figure 37

Periclimenaeus schmitti Holthuis, 1951a, p. 90, pl. 27, figs. a–m.

Recognition characters.—Rostrum short, straight, or somewhat decurved, not reaching to end of basal article of antennular peduncle; upper margin bearing one or two teeth, exclusive of upturned tip; lower margin convex, unarmed. Carapace smooth; postorbital ridge paralleling orbit, extending from strong antennal spine dorsally and becoming gradually obsolete; anterolateral angle broadly rounded, produced forward. Eyes well developed, cornea globular, shorter and narrower than eyestalk. Basal article of antennular peduncle with short, broad, blunt tipped stylocerite reaching about to middle of article; outer margin with blunt angle at level of stylocerite tip, concave beyond angle, anterolateral angle of article with rather large tooth; second and third articles short; upper antennular flagellum with three fused joints, free part of short ramus with one short joint. Antennal scale broadly ovate; outer margin nearly straight, with no terminal tooth.

First leg with carpus and chela extending beyond antennal scale; chela slender, fingers two-thirds length of palm, unarmed, carpus about as long as chela, slightly shorter than merus. Second legs unequal, both reaching with chela and part of carpus beyond antennal scale. Larger second leg heavy, fingers slightly less than half as long as palm, inwardly curved; upper margin of dactyl broadly rounded, cutting edge finely denticulate distally, with large rectangular-shaped tooth fitting into pit on immovable finger when closed; fixed finger with strong, narrow tooth at inner margin of pit; palm swollen, covered with a number of small scalelike tubercles; carpus conical, about one-fourth length of palm; merus about one-third length of palm, sometimes with small tubercles at lower edge. Smaller second leg with fingers straight, slightly shorter than one-third length of palm; cutting edge of dactyl denticulate throughout, that of fixed finger straight; tubercles on palm fewer than on opposite member. Third leg with propodus and part of

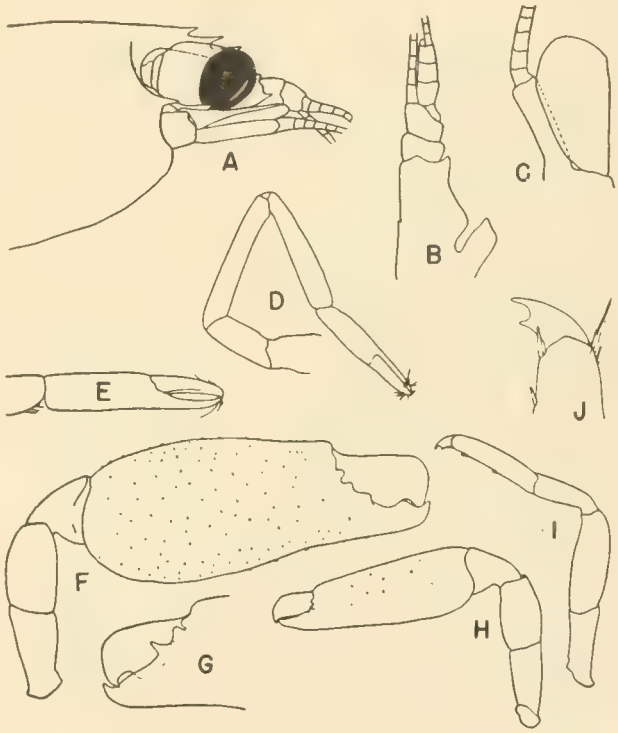

FIGURE 37.—*Periclimenaeus schmitti* Holthuis. A, anterior part of body in lateral view, × 17; B, antennule, × 22.5; C, antenna, × 22.5; D, first leg, × 22.5; E, chela of first leg, × 33.5; F, larger second leg, outside, × 15; G, fingers of larger second leg, inside, × 15; H, smaller second leg, × 15; I, third leg, × 15; J. dactyl of third leg, × 56.5 (after Holthuis, 1951a).

carpus reaching beyond antennal scale, dactyl short, distinctly bifurcate.

Abdomen smooth; pleura of first five segments rounded; sixth segment about as long as fifth and about two-thirds length of telson. Telson with two pairs of small dorsal spines somewhat removed from lateral margin, placed at one-third and two-thirds length; six spines on posterior margin placed in one row, intermediate spines longest. Uropods broadly ovate, exopod with outer margin ending in a tooth flanked medially by a movable spine.

Measurements.—Length of body: ovigerous female, 20 mm.

Variations.—Specimens with a single rostral tooth are young.

Habitat.—Shallow water.

Type locality.—Tortugas, Fla.

Known range.—Bogue Sound, N.C.; Tortugas, Fla.

Remarks.—Two specimens from North Carolina were taken August 16, 1957, in a nighttime surface plankton tow on flood tide near Beaufort Inlet. Though these have intermediate spines on the telson longer than the other terminal pairs, they agree well with specimens of *P. schmitti* from Tortugas.

Periclimenaeus wilsoni (Hay)

Figure 38

Coralliocaris wilsoni Hay, 1917, p. 71.—Hay and Shore, 1918, p. 394, text-fig. 13; pl. 27, fig. 8.

Periclimenaeus wilsoni: Holthuis, 1951a, p. 103, pl. 31, figs. a–m; pl. 32, figs. b–c (rev.).

Recognition characters.—Rostrum nearly straight or somewhat decurved, almost reaching end of antennular peduncle; upper margin somewhat convex, bearing 10 to 12 regularly spaced teeth, first tooth directly over or immediately behind orbital margin; lower margin straight or concave, unarmed. Carapace smooth with only an antennal spine placed close to acute lower orbital angle; postorbital ridge paralleling orbit indistinct; anterolateral angle somewhat anteriorly produced, broadly rounded. Eyes well developed. Stylocerite of antennular peduncle broad, short, and pointed, almost reaching middle of basal article; outer margin of basal article with a blunt angle near tip of stylocerite, concave beyond angle, ending in a strong tooth; second

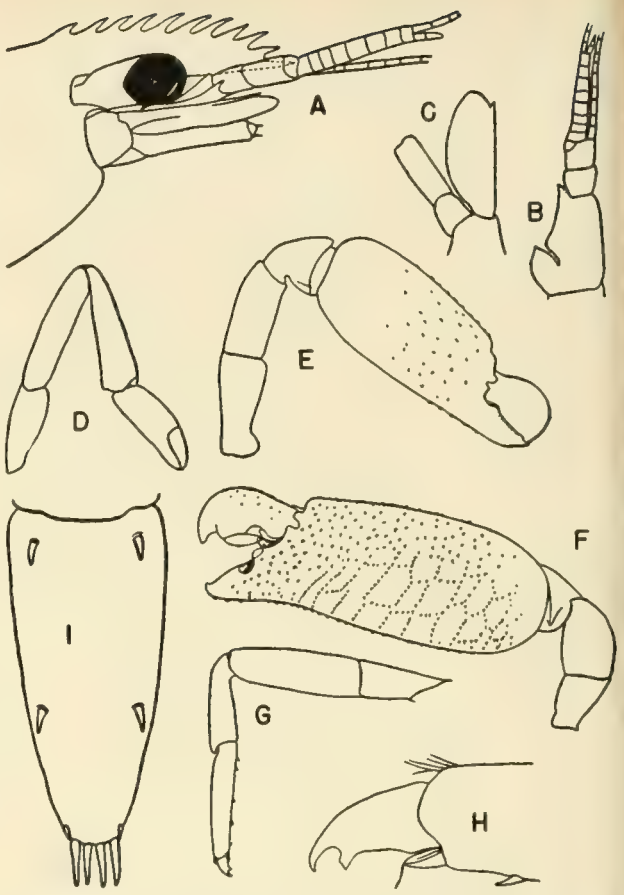

FIGURE 38.—*Periclimenaeus wilsoni* (Hay). A, anterior part of body in lateral view, × 11.5; B, antennule, × 9.5; C, antenna, × 9.5; D, first leg, × 9.5; E, smaller second leg, × 9.5; F, larger second leg, × 4.5; G, third leg, × 9.5; H, dactyl of third leg, × 56; I, telson in dorsal view, × 17 (after Holthuis, 1951a).

and third antennular articles about same size; upper antennular flagellum with six to nine fused joints; free part of short ramus with two joints. Antennal scale a little longer than antennal peduncle; outer margin straight, ending in a small spine; lamella broadest proximally.

First legs with carpus and chela extending beyond tip of antennal scale; chela rather thickset; fingers shorter than palm, unarmed; carpus about as long as merus. Second legs strong, unequal, with part of carpus and chela extending beyond tip of antennal scale. Larger second legs with chela almost equal to bulk of body; fingers inwardly curved, somewhat less than half length of palm; dactyl with upper margin convex, cut-

ting edge with large rectangular tooth fitting into pit on immovable finger when closed; immovable finger with distinct tooth at inner margin of pit; palm swollen, tuberculate at base and on base of fingers, tubercles on proximal lower part of palm arranged in rows or honeycomb pattern; carpus smooth, short, cup-shaped; merus about one-third length of palm. Smaller second leg much as larger one in general shape; palm somewhat swollen, with scattered tubercles anteriorly. Third leg with greater part of propodus reaching beyond tip of antennal scale; dactyl short, broad, bifurcate.

Abdomen smooth; pleura of first five segments broadly rounded; sixth segment half length of telson. Telson with two pairs of dorsal spines somewhat removed from lateral margin, anterior pair close to anterior margin, posterior pair slightly behind midlength; posterior margin with three pairs of spines, outer pair short and located in advance of larger intermediate and inner pairs. Uropods broadly ovate, outer margin of exopod ending in a tooth flanked medially by a movable spine.

Measurements.—Length of body: male, 20 mm.; ovigerous females, 16 to 20 mm.

Variations.—Juveniles may have a shorter rostrum with fewer dorsal teeth, and in some specimens the second chelae may be smooth.

Color.—Clear, milky white; integument so transparent that color of internal organs is plainly visible; egg masses light bluish green.

Habitat.—This species is known to live in sponges in coastal waters in company with *Synalpheus longicarpus* and *S. townsendi;* 10–40 fathoms.

Type locality.—Fishing grounds, 20 miles off Beaufort Inlet, N.C.

Known range.—Off Beaufort, N.C.; off Loggerhead Key, near Tortugas, and Franklin County, Fla.

Remarks.—Ovigerous females have been reported from Florida in July and North Carolina in August. Gurney and Lebour (1941) described the last larval stage of a shrimp doubtfully referred to *P. wilsoni.*

When disturbed, the animals are able to make a snapping sound with the large chela quite as loud as that made by one of the true snapping shrimps.

Genus *Pontonia* Latreille, 1829

Holthuis, 1951a, p. 115.—Hemming, 1958b, p. 124.

Pontonia domestica Gibbes

Figure 39

Pontonia domestica Gibbes, 1850, p. 196.—Holthuis, 1951a, p. 122, pl. 38, figs. a–j (rev.).

Recognition characters.—Rostrum depressed, rather narrowly triangular, decurved; reaching to second article of antennular peduncle; tip acute

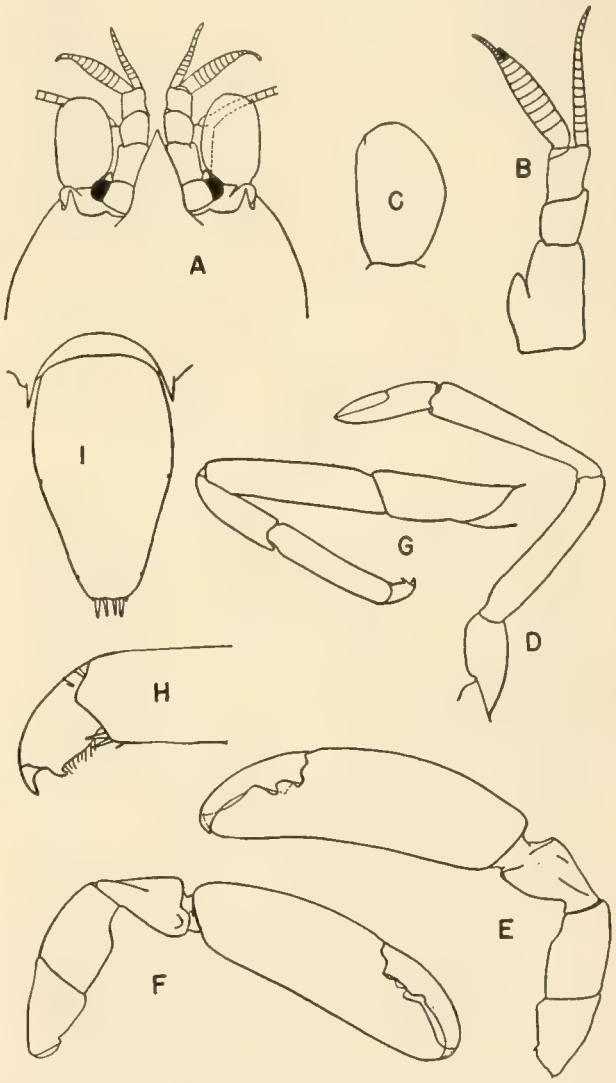

FIGURE 39.—*Pontonia domestica* Gibbes. A, anterior part of body in dorsal view, × 5.5; B, antennule, × 7.5; C, antennal scale, × 7.5; D, first leg, × 5.5; E, larger second leg, × 2.5; F, smaller second leg, × 2.5; G, third leg, × 5.5; H, dactyl of third leg, × 20; I, telson in dorsal view, × 9.1 (after Holthuis, 1951a).

in dorsal and lateral view, flat dorsally; an inconspicuous longitudinal carina ventrally; an inconspicuous dorsal and ventral tooth near tip with tuft of long hairs between upper tooth and apex. Carapace with lower orbital angle bluntly triangular, a strong antennal spine below angle; anterolateral angle broadly rounded and anteriorly produced. Eyes well developed, not reaching laterally to antennal spine. Antennular peduncle with stylocerite broad, bluntly pointed; anterolateral angle of basal article produced forward, rounded; third article longer than second; upper antennular flagellum with 7–10 fused joints; short ramus with 2 or 3 joints. Antennal scale broadly oval, outer margin a little convex, terminal tooth small, exceeded by lamella; antennal peduncle reaching beyond middle of scale.

First leg with carpus and chela reaching beyond antennal scale; fingers of chela somewhat longer than palm; carpus as long as merus. Second legs strong, unequal in size and shape; carpus and chela reaching beyond antennal scale. On one leg, fingers about half length of palm; immovable finger somewhat higher than dactyl and bearing two large teeth on cutting edge, anterior tooth triangular, at middle of edge, posterior tooth truncate with crenulate margin; dactyl with one tooth; palm with upper and lower margin somewhat compressed, surface appearing minutely roughened under magnification; carpus short, conical, with a depression above and a knob below; merus a little longer than carpus. Other second leg much as above but with relatively longer fingers; immovable finger higher in comparison to dactyl; teeth smaller and carpus more slender. Remaining legs with bifurcate dactyls.

Abdomen with first five pleura broadly rounded. Sixth segment with pleura and posterolateral angle ending in slender, sharp spines; slightly longer than fifth segment. Telson half again as long as fifth segment; two dorsal pairs of spines on lateral margin of telson small, almost invisible; anterior pair about in middle, posterior pair closer to posterior border than to anterior pair; posterior border with three pairs of spines in a row; inner two pairs equal in length, outer pair smaller; uropods broadly ovate, outer margin of exopod ending in blunt angle with small movable spine at tip.

Measurements.—Length of body: male 32 mm.

Color.—Translucent white.

Habitat.—The species lives commensally in lamellibranch mollusks in coastal waters and has been recorded from *Atrina seminuda*, *A. serrata*, and *Pecten* sp. (Holthuis, 1951a); shallow water to 23 fathoms.

Type locality.—South Carolina.

Known range.—Atlantic Beach near Beaufort Inlet, N.C., to Chandeleur Islands, La.; Bahamas; Madeira.

Remarks.—Brooks and Herrick (1892) illustrated a section through the segmenting egg of *Pontonia domestica* on plate 28.

Pontonia margarita Smith

Figure 40

Pontonia margarita Smith, 1869c, p. 245.—Holthuis, 1951a, p. 137, pl. 43, figs. a–l; pl. 44, figs. a–h (rev.).

Recognition characters.—Rostrum depressed and decurved, dorsally flat and triangular; tip reaching to end of basal article of antennular peduncle or slightly beyond; an inconspicuous dorsal and ventral tooth near tip with small tuft of hairs between upper tooth and apex; a longitudinal median carina ventrally. Carapace smooth; with strong antennal spine located well below narrowly rounded lower orbital angle; anterolateral angle broadly rounded and anteriorly produced. Eyes somewhat larger than in *P. domestica*, reaching laterally beyond antennal spine. Basal article of antennular peduncle with blunt-pointed stylocerite more or less pressed against outer border; anterolateral angle of article produced forward, rounded; upper antennular flagellum short, thick, curved backward; fused part with six or seven joints; short ramus with two joints. Antennal scale with convex outer margin ending in small inwardly curved distal tooth, lamella far exceeding tooth.

First leg with half or more than half of carpus reaching beyond antennal scale; fingers longer than palm, unarmed; carpus longer than merus. Second legs unequal in size but similar in shape. Larger leg with fingers a little over half length of palm; palm twice as long as deep, somewhat inflated; dactyl narrower than immovable finger and bearing one large tooth slightly behind middle; cutting edge of immovable finger with two large teeth fitting on each side of opposed dactylar

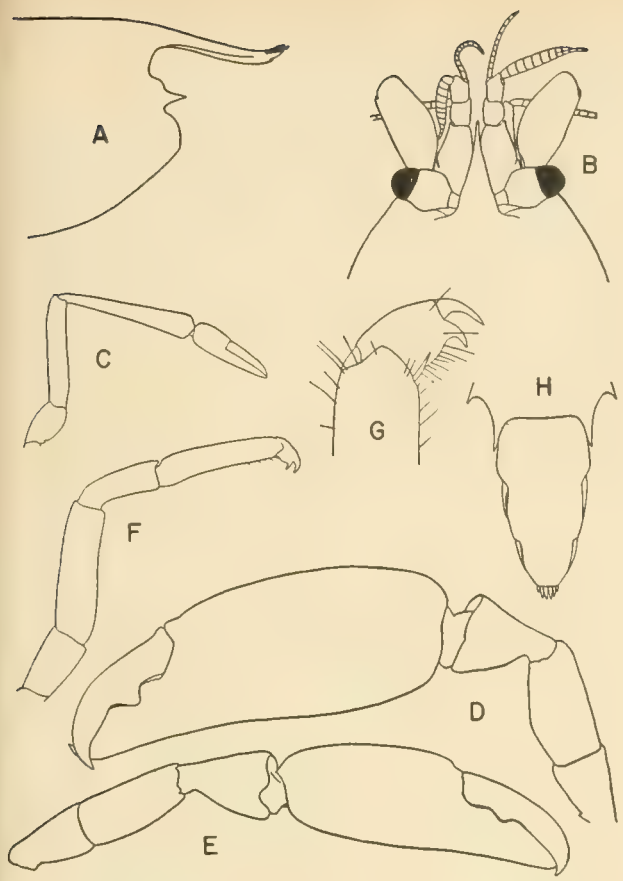

FIGURE 40.—*Pontonia margarita* Smith. A, anterior part of carapace in lateral view, × 11.5; B, anterior part of body in dorsal view, × 11.5; C, first leg, × 5.9; D, larger second leg, × 6; E, smaller second leg, × 6; F, third leg, × 9.5; G, dactyl of third leg, × 35; H, telson in dorsal view, × 11.5 (after Holthuis, 1951a).

tooth and separated by a hole on inner side of edge, posterior tooth with denticles at apex; carpus shorter than merus, conical. Smaller second leg resembling larger except for relatively longer fingers. Dactyls of last three walking legs bifurcate.

Abdomen with pleura of first five segments broadly rounded, of sixth ending in a strong spine overlapping base of uropods. Sixth segment a little more than half length of telson. Telson with two pairs of large dorsal spines placed laterally, and at one-third and two-thirds of length; posterior border with three pairs of spines in a row, inner two pairs equal, outer pair smaller. Uropods broadly ovate, exopods ending in a minute movable spine on outer margin.

Measurements.—Length of body: male, 19 mm.; ovigerous females, 17 to 27 mm.

Color.—Glassy, translucent; internal organs clearly visible; ovigerous females with two colors of eggs, one with light, muddy green eggs and ovarian ova of same color, another with pale orange eggs (from specimens taken in *Aequipecten gibbus* off Drum Inlet, N.C., in 20-fathom water, April 14, 1960).

Habitat.—The species lives commensally in lamellibranch mollusks in coastal waters. It has been found in *Aequipecten gibbus* and *Pteria colymbus* in North Carolina, and in the pearl oyster *Pinctada fimbriata* on the west American coast; tidal flats to 33 fathoms.

Type locality.—Bay of Panama.

Known range.—Atlantic coast: Drum Inlet to Beaufort Inlet, N.C.; east and west Florida. Pacific coast: Gulf of California to Colombia; Galapagos Islands.

Remarks.—Ovigerous females have been taken in North Carolina in January and April.

Genus ***Neopontonides*** Holthuis, 1951

Holthuis, 1951a, p. 189.

Neopontonides beaufortensis (Borradaile)

Figure 41

Periclimenes beaufortensis Borradaile, 1920, p. 132.
Neopontonides beaufortensis: Holthuis, 1951a, p. 190, pl. 59, figs. g–k; pl. 60, figs. a–k (rev.).

Recognition characters.—Rostrum slender, straight; a little shorter than antennular peduncle; laterally compressed but broadened at base, covering eyestalks, lateral margin of widened base not merging with obital margin; upper margin with none to five teeth, most proximal teeth, when present, in front of posterior margin of orbit on a crest, crest remaining visible in absence of teeth; lower margin unarmed. Carapace smooth or somewhat areolated; anterior margin of carapace with lower angle of orbit produced in a rounded lobe; antennal spine strong, located considerably below orbit; a rounded lobe slightly below antennal spine followed by an emargination ending in a produced anterolateral angle; hepatic and supraorbital spines absent. Eyes large, reaching almost to end of rostrum. Basal article of antennular peduncle with sty-

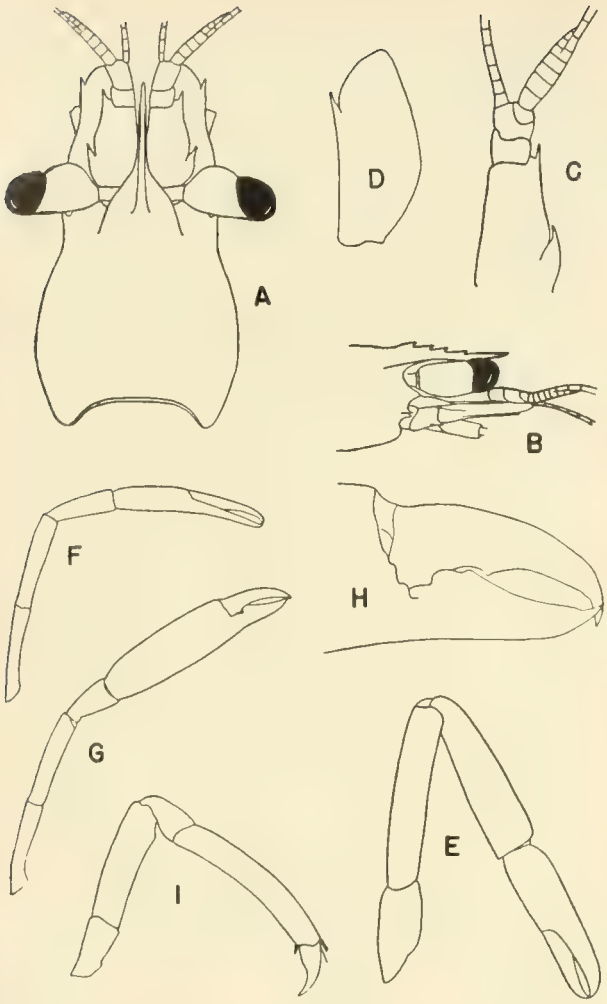

FIGURE 41.—*Neopontonides beaufortensis* (Borradaile). A, anterior part of body in dorsal view, × 19.5; B, anterior part of body in lateral view, × 13; C, antennule, × 26; D, antennal scale, × 26; E, first leg, × 39; F, smaller second leg, × 26; G, larger second leg, × 26; H, fingers of larger second leg, × 65; I, third leg, × 26 (after Holthuis, 1951a).

locerite rather broad, ending in slender point reaching almost to middle of article; outer margin of article slightly concave ending in strong anterolateral spine reaching end of second article; upper antennular flagellum with rami fused for two to four joints; short ramus with two to four free joints. Antennal scale reaching beyond antennular peduncle; concave outer margin ending in strong tooth; lamella exceeding tooth; a small lateral tooth at base; antennal peduncle reaching about to middle of scale.

First leg reaching beyond end of antennal scale; fingers slightly shorter than palm, unarmed, slightly agape; carpus about as long as merus. Second legs unequal. Part of palm of larger leg exceeding antennal scale; fingers half or less length of palm, dactyl with two, immovable finger with one tooth on cutting edge; palm slightly swollen; carpus short, conical; merus about twice length of carpus. Smaller second leg with fingers as long as palm, slender, unarmed; carpus nearly as long as palm. Third leg with heavy, simple dactyl.

Abdomen smooth, all pleura broadly rounded. Sixth segment as long as telson. Telson with two pairs of dorsolateral spines; posterior pair midway between anterior pair and tip; three pairs of spines on posterior border, intermediate pair less than twice length of inner pair. Uropods elongate; outer margin of exopod ending in a tooth flanked medially by a movable spine.

Measurements.—Length of body: male, 9 mm.; ovigerous females, 7 to 9 mm.

Variations.—In young specimens, the legs are relatively shorter than in adults, and the larger second leg resembles the smaller second leg of adults.

Color.—Nearly transparent, but with faint coloration of *Leptogorgia* from which individuals are taken (yellow or orange).

Habitat.—This species is found in coastal waters where it lives in association with *Leptogorgia;* surface to a few fathoms.

Type locality.—Beaufort, N.C.

Known range.—Beaufort, N.C., to Grand Isle, La. (Dawson, 1963); Caledonia Bay, Panama; Antigua.

Remarks.—Ovigerous females have been taken in Bogue Sound near Beaufort Inlet, N.C., in August and November, in Panama in April, and in Antigua in May.

Subfamily **Palaemoninae**

Upper antennular flagellum with both rami fused in basal part. Appendix masculina generally present on second pleopod of male, appendix interna on second pleopod of female. Pleurobranch present on third maxilliped. Posterior margin of telson with two pairs of spines and one or more pairs of setae (Holthuis, 1952).

KEY TO GENERA AND SPECIES IN THE CAROLINAS

(Holthuis, 1952, modified)

a. Hepatic spine present, branchiostegal spine absent; chelate second legs enlarged and greatly elongated.
  b. Dactyls of last three legs bifurcate; marine *Brachycarpus biunguiculatus* (p. 51).
  bb. Dactyls of last three legs simple; fresh or brackish water ---------- *Macrobrachium* (p. 52).
    c. Fingers of chelae on second legs thickly pubescent throughout length; rostrum with teeth extending up to tip ---------- *M. acanthurus* (p. 52).
    cc. Fingers of chelae on second legs with scattered hairs, except thicker on fingers along cutting edges; rostrum with toothless daggerlike tip *M. ohione* (p. 54).

aa. Hepatic spine absent, branchiostegal spine present; chelate second legs not greatly enlarged.
  b. Mandible with a palp ---*Leander tenuicornis* (p. 55).
  bb. Mandible without a palp ----*Palaemonetes* (p. 56).
    c. Carpus of second leg in adult female shorter than palm, in males slightly longer or shorter (1.1 times) than palm; dactyl of second leg with two, immovable finger with one tooth on cutting edge; rostrum with first two teeth of dorsal margin behind orbit, dorsal rostral teeth reaching to apex, lower margin with three to five teeth *P. vulgaris* (p. 56).
    cc. Carpus of second leg in adult female much longer than palm (1.3 to 1.5 times), in males almost as long as whole chela; dactyl of second leg with a single tooth or without teeth, immovable finger without teeth on cutting edge; rostrum with only one dorsal tooth behind orbit.
      d. Dorsal teeth of rostrum reaching up to apex, apex often bifurcate; lower margin of rostrum with four or five, seldom three teeth; dactyl of second leg with one distinct tooth on cutting edge ---------- *P. intermedius* (p. 58).
      dd. Dorsal and ventral margins of rostrum with an unarmed stretch before dagger-shaped tip; lower margin of rostrum with two to four, generally three, teeth; fingers of second leg without teeth on cutting edges ---------- *P. pugio* (p. 59).

Genus *Brachycarpus* Bate, 1888

Holthuis, 1952, p. 2.—Hemming, 1958b, p. 154.

Brachycarpus biungiuculatus (Lucas)

Figure 42

Palaemon biunguiculatus Lucas, 1849, p. 45, pl. 4, fig. 4.
Brachycarpus biunguiculatus: Holthuis, 1952, p. 3, pl. 1, figs. a–q (rev.).

Recognition characters.—Rostrum well developed, rather high, directed straight forward, reaching about to end of antennal scale; upper margin with seven (seldom eight) teeth, first two teeth placed behind orbit with first tooth at about midlength of carapace; lower margin with three (seldom two or four) teeth. Carapace smooth; antennal and hepatic spines present; a strong postorbital ridge paralleling orbit. Eyes well developed. Basal article of antennular peduncle with anterolateral spine strong, reaching beyond second article of peduncle; stylocerite small, acute, closely appressed to article; rami of inner antennular flagellum fused for 8 to 23 joints; free part

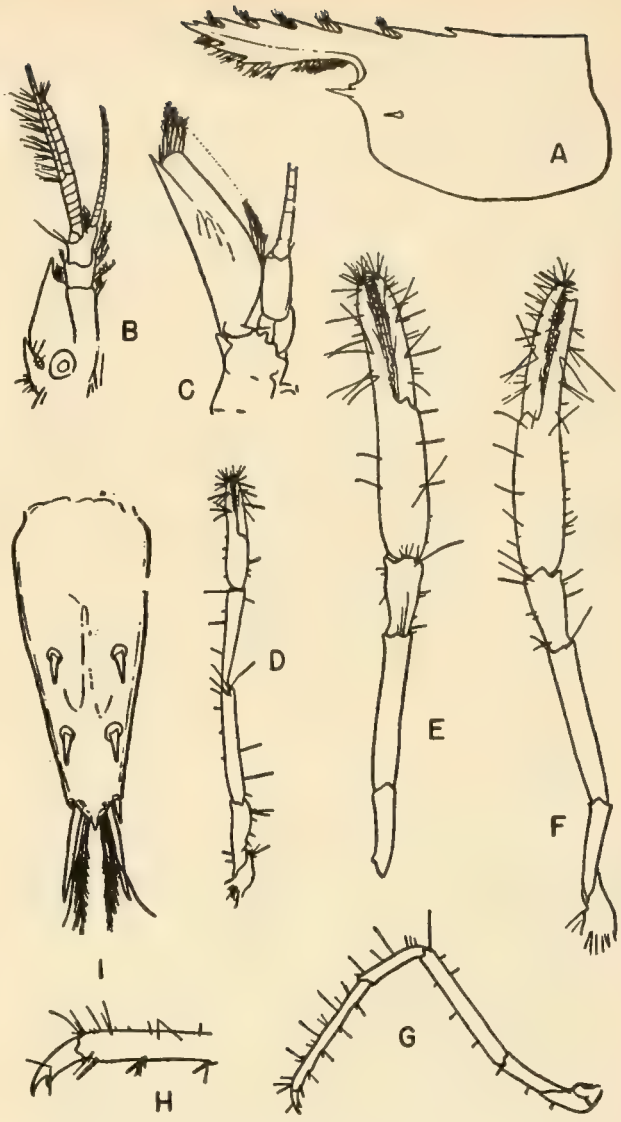

FIGURE 42.—*Brachycarpus biunguiculatus* (Lucas). A, carapace in lateral view, × 6; B, antennule, × 7; C, antenna, × 7; D, first leg, × 6; E, left second leg, × 6; F, right second leg, × 6; G, third leg, × 6; H, dactyl of third leg, × 16; I, telson, × 15 (after Schmitt, 1939).

of shorter ramus about as long as fused portion. Antennal scale about three times longer than broad, outer margin concave, terminal spine overreaching lamella.

First legs slender; fingers of chelae longer than palm; carpus longer than chela. Second legs much stronger than first; smooth; part of carpus extending beyond antennal scale; fingers slightly shorter than palm, but in adult males sometimes only half length of palm, cutting edge of dactyl with two to four, immovable finger with two small teeth in proximal part, adult males with fingers widely agape, opening hairy; carpus short, cup-shaped, half length of merus. Last three legs slender, dactyls bifurcate, propodi with spines present on posterior margin.

Abdomen smooth, pleura of fourth and fifth segments pointed. Telson with two pairs of dorsal and two pairs of posterior spines; numerous setae between inner posterior spines. Appendix interna present on first pleopods in males, missing in females.

Measurements.—Length of body: 65 mm. (Holthuis, 1952).

Variations.—Dorsal spines on the telson are sometimes not placed in symmetrical pairs and may be asymmetrically doubled.

Color.—Living individuals: body dark blue green mottled with white; palm of chela uniform blue green, fingers barred; fringes of antennules, antennae, antennal scale and tail fan orange; some individuals colorless, with tawny-tinged spots. Preserved specimens: pale brownish yellow, tips of fingers brownish red preceded by colorless band, then a fainter band of brownish red; antennular flagella red with white rings at articulations between joints (Holthuis, 1952).

Habitat.—Found near shore among corals or rocks, and on sea buoys; surface to 4 fathoms.

Type locality.—Oran and Bône, Algeria.

Known range.—Virtually pantropical; East and West American coasts, Mediterranean; West Africa; and Indo-Pacific region. Western Atlantic distribution: Cape Fear, N.C., through West Indies to Curaçao and Old Providence Island; Bermuda.

Remarks.—Gurney and Lebour (1941) described a complete series of 11 larval stages and a postlarval stage of this species from Bermuda. They pointed out that the larval life of this form may be indefinite in length and number of developmental stages, and that this feature of development may account for the wide distribution of the species. Gurney (1943a) noted proportional changes in growth of the segments of the second legs in the last larval stage, first postlarval stage, and adult female.

Genus *Macrobrachium* Bate, 1888

Holthuis, 1952, p. 10.

Macrobrachium acanthurus (Wiegmann)

Figures 43–44

Palaemon acanthrus Wiegmann, 1836, p. 150.
Macrobrachium acanthurus: Holthuis, 1952, p. 45, pl. 9, figs. a–b (rev.).

Recognition characters.—Rostrum almost straight, reaching slightly beyond antennal scale; upper margin slightly arched basally, with 9–11 teeth, proximals closer together than distals, first 2 teeth on carapace behind orbit, second tooth sometimes partly over posterior margin of orbit and separated from first tooth by distance greater than that between other proximal teeth; lower margin with 4 to 7 (generally 6) teeth, proximals closer together than distals. Carapace smooth, with short hairs especially on anterolateral region; antennal spine a little below orbit and slightly removed from margin; hepatic spine behind and a little below antennal spine. Antennal scale about three times longer than broad; outer margin straight or convex.

First legs with chela and sometimes part of carpus reaching beyond scale; fingers as long as palm; carpus one-third longer than merus. Second legs equal, with carpus and sometimes part of merus reaching beyond scale; fingers slender, thickly pubescent throughout length, slightly shorter than palm, cutting edges with a tooth on each finger in proximal quarter (that of dactyl more advanced) preceded by row of about four denticles; palm elongate, cylindrical, with several longitudinal rows of spinules largest and widest apart on inner and lower regions; carpus and merus spinulose like palm. Articles of last three walking legs with numerous densely placed small spinules.

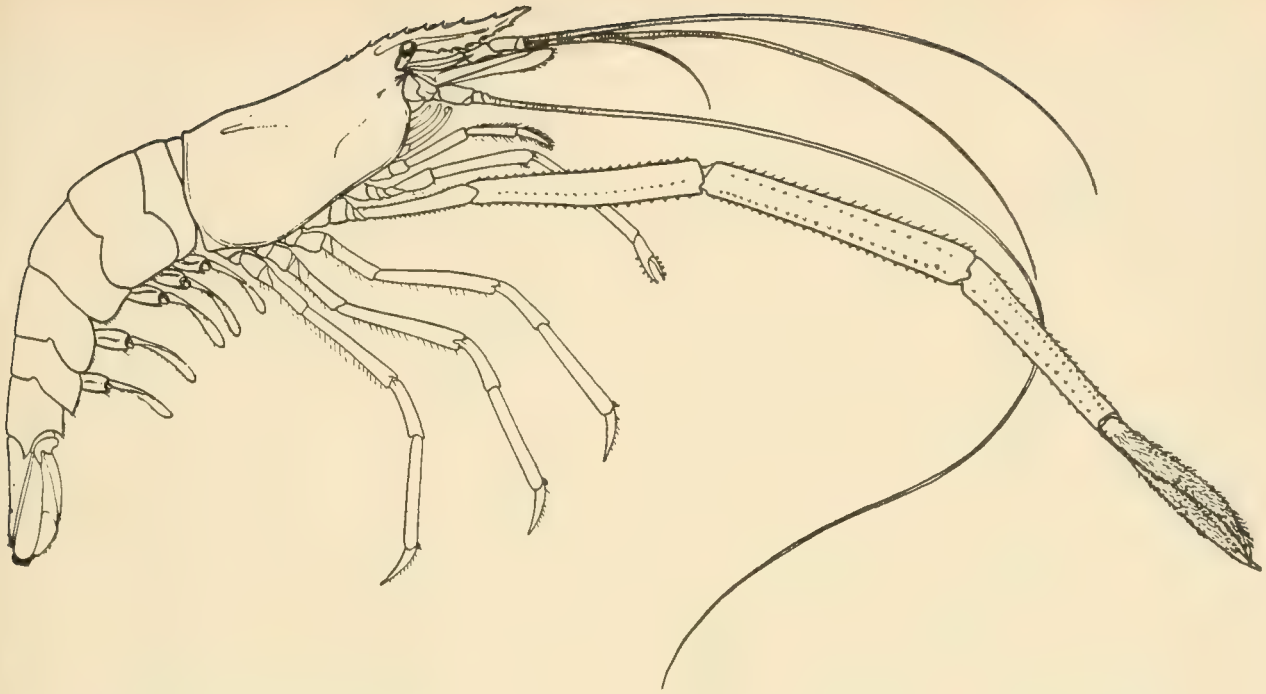

FIGURE 43.—*Macrobrachium acanthurus* (Wiegmann). Animal in lateral view (after Hedgpeth, 1949).

Abdomen smooth; pleura of fifth segment ending in an acute point. Telson 1.5 times length of sixth segment, with pairs of dorsal spines at middle and three-fourths of length; posterior margin ending in sharp median point flanked by two pairs of spinules, inner pair overreaching median point.

Measurements.—Length of body: male, 166 mm.; ovigerous females, 36 to 110 mm.

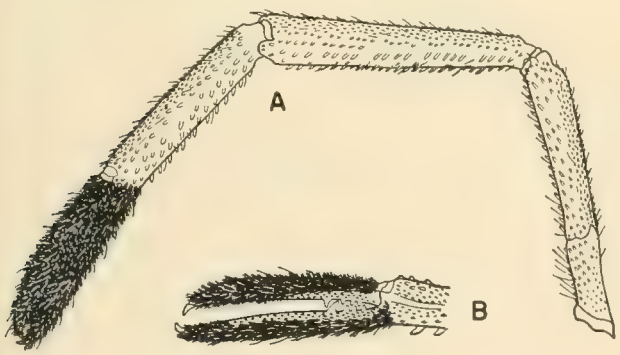

FIGURE 44.—*Macrobrachium acanthurus* (Wiegmann). A, second leg of adult male; B, fingers of second leg of adult male (part of hairs removed); A, B, × 0.75 (after Holthuis, 1952).

Variations.—The rostrum may vary in length and shape. Adult females and young males have second legs shorter, more slender, less spinulose and pubescent than adult males.

Color.—Green or pale yellow with red speckles; carapace with middorsal stripe of red or brownish orange and occasionally with irregular red bands laterally; chelipeds greenish becoming blue distally, articulations orange; abdomen with middorsal stripe similar to carapace, pleura green with blue edges and striped with red; eggs green (Hedgpeth, 1949; Schmitt in Holthuis, 1952).

Habitat.—The species lives in coastal rivers and bays, usually near brackish water, but sometimes quite far upstream; 97 miles from mouth of Rio Grande River in Texas (Hedgpeth, 1949).

Type locality.—Brazilian coast.

Known range.—Neuse River estuary, N.C., to Rio Grande do Sul, Brazil; West Indies.

Remarks.—This species probably has a later breeding season than *Macrobrachium ohione* (Hedgpeth, 1949). The recent discovery of *M. acanthurus* in the Neuse River estuary of North Carolina may indicate an active northward extension of range similar to the case of *M. ohione*.

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Macrobrachium ohione (Smith)

Figure 45

Palaemon Ohionis Smith, 1874, p. 640.
Macrobrachium ohione: Holthuis, 1952, p. 62, pl. 14, fig. b (rev.).

Recognition characters.—Rostrum high and straight, tip curving somewhat upward and reaching to between end of antennular peduncle and end of antennal scale; upper margin with 9 to 13 teeth, 3 or 4 teeth behind orbit, first 3 more widely separated than remainder; lower margin with 1 to 3 teeth; distal two-fifths of rostrum unarmed. Carapace smooth; antennal spine slightly remote from anterior margin; hepatic spine below antennal spine. Antennal scale about 2.5 times longer than broad; outer margin straight or slightly concave.

First legs with chelae reaching beyond scale; chelae slender; fingers about as long as palm; carpus twice length of chela. Second legs in adult female stronger than in male, with carpus and chela reaching beyond scale; fingers somewhat shorter than palm, cutting edges pubescent and with four to eight small denticles of equal size on proximal half, remainder of surface with scattered hairs; palm elongate, cylindrical, entirely pubescent, most conspicuous pubescence along lower surface; carpus, merus, and palm of equal length, these articles and fingers with longitudinal rows of small spinules; carpus most pubescent anteroventrally; merus somewhat pubescent anteroventrally.

Abdomen smooth; pleura of fifth segment ending in acute point. Telson about 1.5 times length of sixth segment; pairs of dorsal spines at middle and three-fourths of length; posterior margin ending in an acute tip overreached by inner pair of posterior spines.

Measurements.—Length of body: male, 68 mm.; female, 102 mm.

Variations.—Juveniles (10 mm. and larger) have the same number of rostral spines as adults but fewer spines behind the orbit. In such juveniles, the hepatic spine is very close to the anterior margin of the carapace, similar in position to a branchiostegal spine.

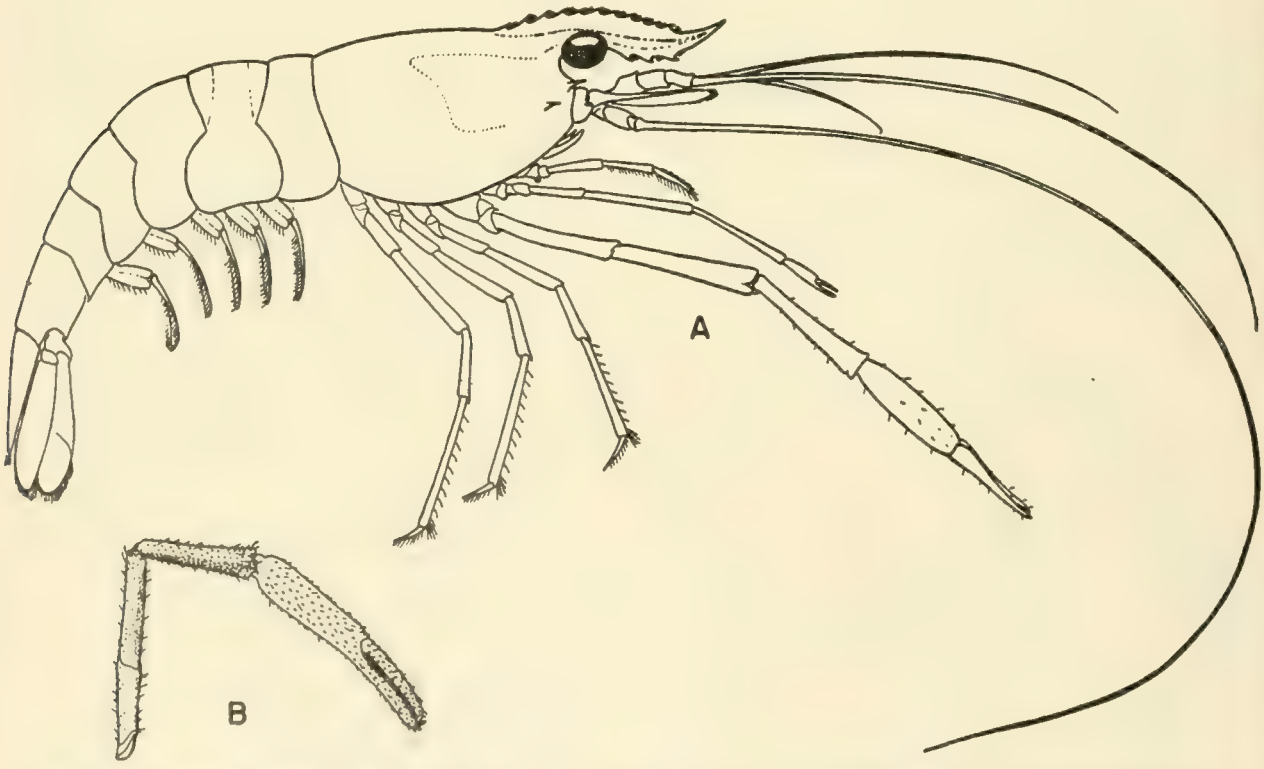

FIGURE 45.—*Macrobrachium ohione* (Smith). A, animal in lateral view (after Hedgpeth, 1949); B, second leg of adult male (after Holthuis, 1952).

Color.—Pale gray flecked with small blue spots; uropods pale blue (Hedgpeth, 1949).

Habitat.—This species lives in rivers and estuaries.

Type locality.—Ohio River at Cannelton, Ind.

Known range.—A narrow zone along Atlantic seaboard from James River, Hopewell, Va. (Hobbs and Massmann, 1952), to southern Georgia; widespread from coastal Alabama to Aransas Bay, Tex.; Mississippi River and tributaries upstream to McCurtain County, Okla.; Fort Smith, Ark.; St. Louis, Mo.; Washington County, Ohio.

Remarks.—This species is distributed chiefly in brackish and fresh water, ranging far inland in the Mississippi River drainage. It is abundant enough, especially in Louisiana, to provide a fishery of some importance though the exact magnitude is not known. Gunter (1937) described the Louisiana fishery and gave information on ecology of the species. Commercially, the shrimp are taken in traps made of wooden slats, similar to lobster traps, baited with meat scraps or cottonseed cake. The shrimp are sometimes captured by lifting submerged willow branches from the water and catching the animals as they drop off. Such catches are best made at night. Commercial shrimping is done in the warmer months, as the animals are scarce in winter. The shrimp will attack fish kept in live boxes in the river, and, though the feeding habits of the species are not known completely, the animals are thought to be primarily carnivorous.

During a period of study from November to early July, Gunter found that ovigerous females first appeared in mid-April, and egg-bearing females were still present when the work was terminated in July. Ovigerous females have been found in April and May in North Carolina. McCormick (1934) stated that eggs in various stages of development were found in females at the same time that they were in berry, which indicates a long egg-laying season. Gunter found females to outnumber males by more than 3 to 1. However, this ratio varied. When females were carrying eggs, males made up only 9 percent of the captured individuals, but prior to the egg-laying season males made up 31.8 percent of the total. He concluded that this indicated a change in sex ratio at the egg-bearing period.

Thirteen percent of the females caught were ovigerous, and these ranged in length from 38 to 76 mm. Eggless females ranged from 23 to 93 mm. in length. From November to December, the population was made up of individuals 60–80 mm. long. In January, shrimp below 30 mm. average length predominated, but from then until April the average length increased to about 50 mm., and thereafter the range of variation widened as smaller animals came into the catch.

Gunter found ovigerous females in bay water with salinities ranging from 1.38 to 14.24 ‰. He noted that when the river was on a rise, with turbidity high, few shrimp were taken in water over 20 feet deep, and these were sometimes dead. He conjectured that because these shrimp were not buried in mud, high turbidity in deep water during flood may have an adverse effect on respiration. Hedgpeth (1949) suggested that silt causing interference with respiration may drive the shrimp from rivers to estuaries during such seasons, but he also suggested that in regions such as the Atlantic seaboard, where the species is apparently a comparatively recent immigrant, it may still depend on bay waters to complete its breeding cycle. In any case, it is thought that these shrimp and other species of the genus move from river to river through the salty estuaries at the river mouths (Gunter, 1937).

Especially interesting is the fact that this species and *M. acanthurus* are forms which may be advanced in the process of moving from the sea to fresh water. Few such examples exist.

Genus ***Leander*** Desmarest, 1849

Holthuis, 1952, p. 167.

Leander tenuicornis (Say)

Figure 46

Palaemon tenuicornis Say, 1818, p. 249.—Hay and Shore, 1918, p. 392, pl. 27, fig. 6.

Leander tenuicornis: Holthuis, 1952, p. 155, pl. 41, figs. a–g; pl. 42, figs. a–f (rev.).

Recognition characters.—Rostrum well developed; high in female, more slender in male; reaching about to end of antennal scale; upper margin with 8 to 14 regularly spaced teeth, first two behind orbit; lower margin with 5 to 7 teeth partially concealed by double row of setae. Carapace smooth; antennal spine present, and a branchiostegal spine placed some distance behind anterior margin; branchiostegal groove absent.

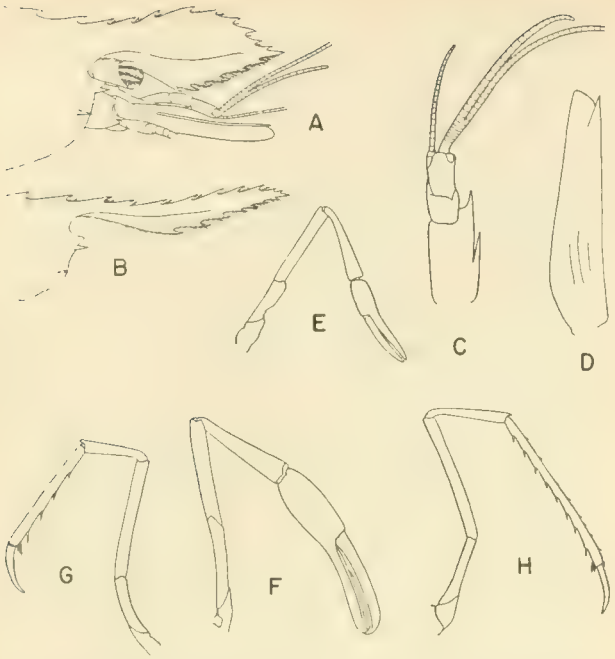

FIGURE 46.—*Leander tenuicornis* (Say). A, anterior part of body of female in lateral view; B, anterior part of carapace of male in lateral view; C, antennule; D, antennal scale; E, first leg; F, second leg; G, third leg; H, fifth leg (after Holthuis, 1952).

Eyes well developed, rounded; two dark-colored bands visible on cornea, especially in fresh material. Basal article of antennule with stylocerite large and pointed, reaching beyond middle of article, and with anterolateral spine reaching almost to end of second article of peduncle, anterior margin of basal article between spine and second article straight or only slightly convex; second and third antennular articles shorter and narrower than first; upper flagellum with fused portion of rami shorter than free portion of shorter ramus. Antennal scale 3 to 5 times longer than broad; outer margin about straight; terminal tooth strong, as long as lamella; antennal peduncle not reaching middle of scale; a strong external spine near base of scale. Mandible with a two-jointed palp.

First pair of legs slender; reaching about to end of scale; fingers longer than palm. Second legs more robust than first, equal in size and shape; chelae reaching beyond scale; fingers longer than slightly swollen palm, cutting edges of fingers entire except for small basal tooth in males; carpus shorter than chela and about as long as merus. Last three legs slender, dactyls simple, slender; propodi armed with posterior spinules; fifth leg more slender than third.

Abdomen smooth; first three pleura broadly rounded; pleura of fourth and fifth segments narrower, ending in a minute, acute tooth. Sixth segment slightly longer than fifth and about two-thirds length of telson. Telson with two pairs of dorsal spines, first pair at midlength, second at three-fourths length; inner of two pairs of posterior spines overreaching acute tip of telson, a pair of strong feathered setae between inner pair of spines.

Measurements.—Length of body: 47 mm.; males generally smaller than females; ovigerous females 26 mm. long have been reported (Holthuis, 1952).

Variations.—Length of the second legs is variable, and the palm of the chela is more swollen in some specimens than in others. Length of the terminal tooth of the antennal scale is variable.

Color.—Green or olive, with opaque spots (Schmitt *in* Holthuis, 1952, for specimens from Tortugas).

Habitat.—Found in floating sargassum, on wharf pilings, and among submerged vegetation.

Type locality.—Newfoundland Banks.

Known range.—Tropical and subtropical waters all over world except for west coast of Americas; Newfoundland Banks to Falkland Islands in western Atlantic (Holthuis, 1952).

Remarks.—Ovigerous females have been observed from July to October in the Carolinas, in June in the middle and western Atlantic (Sivertsen and Holthuis, 1956), and in August at Old Providence Island (Schmitt, 1939). Gurney (1939) described the fifth(?) larval and first postlarval stages and compared them to related forms, with remarks on the statocyst in adults.

Genus ***Palaemonetes*** Heller, 1869

Holthuis, 1952, p. 199. Hemming, 1958b, p. 158

Subgenus ***Palaemonetes*** Heller

Holthuis, 1952, p. 207.

Palaemonetes (Palaemonetes) vulgaris (Say)

Figure 47

Palaemon vulgaris Say, 1818, p. 248.

Palaemonetes carolinus: Hay and Shore, 1918, p. 393, pl. 27, fig. 4.

Palaemonetes (Palaemonetes) vulgaris: Holthuis, 1952, p. 231, pl. 54, figs. f–l (rev.).

Recognition characters.—Rostrum reaching to or slightly beyond end of antennal scale; tip directed upward making upper margin more or less concave; upper margin with 8 to 11 teeth, first 2 teeth behind orbital margin and separated more widely than other proximal teeth, all teeth rather regularly distributed along rostrum but proximals generally closer together than distals, no unarmed space behind tip, tip often bifurcate; lower margin with 3 to 5 (usually 4) teeth. Carapace smooth; antennal spine present; branchiostegal spine on anterior margin just below branchiostegal groove. Eyes well developed. Basal article of antennular peduncle with slender stylocerite reaching slightly beyond middle of article, anterolateral spine of article strong, overreaching rounded anterior margin; upper antennular flagellum with both rami fused for 7 to 9 joints; free part of shorter ramus with 10 to 17 joints, at least 1.5 times as long as fused portion. Antennal scale 3 times longer than broad; terminal tooth strong, reaching almost to end of lamella.

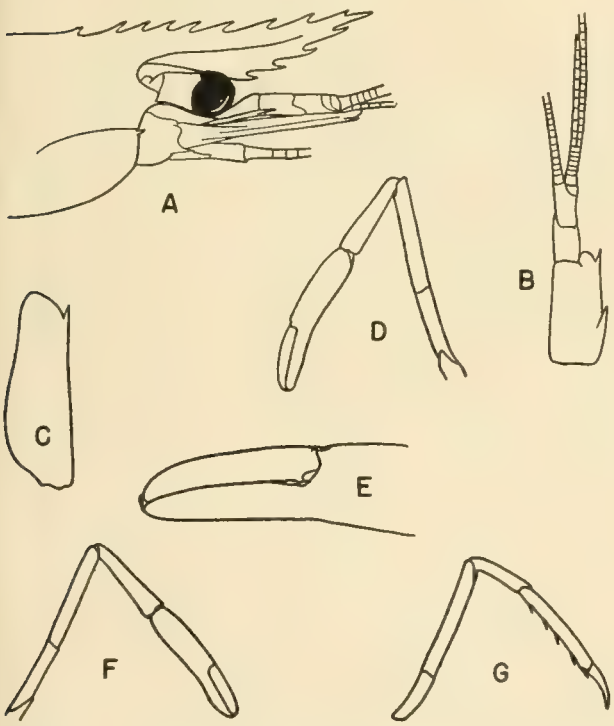

FIGURE 47.—*Palaemonetes* (*Palaemonetes*) *vulgaris* (Say). A, anterior part of body in lateral view; B, antennule; C, antennal scale; D, second leg of female; E, fingers of second leg of female; F, second leg of male; G, third leg; A–G × 5 (after Holthuis, 1952).

First leg usually not reaching to end of antennal scale; fingers about as long as palm; carpus 1.3 to 1.7 times as long as chela and a little longer than merus. Second legs longer and stronger than first, stronger in adult females than in males with fingers and sometimes entire palm reaching beyond scale; fingers a little over half length of palm, cutting edge of dactyl with two small teeth proximally, immovable finger with one similar tooth fitting between those of dactyl; carpus shorter than palm and about three-fourths length of merus. Second legs of male not so large as in female; teeth on fingers indistinct. Third leg with propodus less than twice length of carpus. Fifth leg with propodus about three times length of dactyl, twice as long as carpus.

Abdomen smooth; fifth segment with tip of pleura rectangular or slightly acute. Sixth segment 1.5 times length of fifth, shorter than telson. Telson with two pairs of dorsal spines; anterior pair somewhat behind middle; second pair halfway between these and tip; posterior margin with strong median point flanked by two pairs of spines, inner pair longest and between them two feathered setae. Outer margin of uropodal exopod with a strong terminal tooth flanked by a slender movable spine medially.

Measurements.—Length of body: male, 30 mm.; ovigerous females, 22 to 42 mm.

Color.—Transparent in life.

Habitat.—Estuarine waters, especially in beds of submerged vegetation; water's edge to (rarely) 8 fathoms. Salinity of 3‰ is apparently lethal (Nagabhushanam, 1961).

Type locality.—Atlantic coast of United States.

Known range.—Barnstable County, Mass., to Cameron County, Tex. (from specimens examined by Holthuis, 1952). Literature records: Gaspé, Quebec, Canada, to Rio Champoton and near Progreso, Yucatan, Mexico (Holthuis, 1952).

Remarks.—Correct identification of the species of *Palaemonetes* occurring on the east coast of the United States was not possible until Holthuis (1949) introduced his key. As Holthuis (1952) pointed out, two names, *vulgaris* and *carolinus*, were applied indiscriminately to three species but the description of *carolinus* was actually based on a specimen of *vulgaris*; hence, this name is a synonym of *vulgaris*. With the status of *vulgaris* stabilized, Holthuis went on to show that two

other closely related and newly described species, *intermedius* and *pugio*, occupy much the same habitat and geographic range as *vulgaris*. An unfortunate but natural result of such confusion is that the voluminous literature on "*vulgaris*" undoubtedly concerns all three species in unknown ways, and all such literature must now be viewed with reserve.

Jenner (1955) showed that in the Woods Hole, Mass., region, where much of the experimental work on *Palaemonetes* has been done, both *P. vulgaris* and *P. pugio* occur. He showed that a useful field character for differentiating these two species is color of the eyestalks, the eyestalks of *P. pugio* being generally much more yellow than those of *P. vulgaris*, the latter being more red brown. The source of *Palaemonetes* for the Marine Biological Laboratory is thought to have been principally from the dock where only *P. vulgaris* has been found; hence, Jenner suggested that most of the experimental work at Woods Hole has been correctly referred to *P. vulgaris*. In North Carolina, these eye-color differences are less apparent.

The breeding season for the species in Virginia and the Carolinas extends from April to mid-October. Larval stages of *P. vulgaris* have been described by Broad (1957a) and are summarized below under the account for *P. pugio*.

Burkenroad (1947a) showed that male *P. vulgaris* respond only to females which have molted to breeding form recently. After mating, the female resists further courtship. Males recognize such females only upon contact of the antennae with any surface of the female. The spermatophore will adhere to any part of the integument of either sex, but becomes nonadhesive almost immediately after exposure. Burkenroad stated that the sperm-bearing matrix of the spermatophore dissolves about a half hour or less before spawning, and he thought that some substance freeing the sperm cells must be released by the female at the approach of spawning.

Eggs are released simultaneously from both oviducts in a continuous stream. Fertilization is external and, because sperm cells of decapod crustaceans in general are nonmotile, it was suggested that entry of the sperm cell precedes development of the egg membranes in all decapods. All parts of the eggshell are produced by the ovum or the embryo. The first membrane is developed upon contact with water. The second is developed about half an hour after spawning, and the third about 12 hours after spawning in fertile eggs only. The fourth and last membrane is an embryonic molt skin.

In *Palaemonetes*, the eggs are not adhesive when laid and first adhere to each other about half an hour after spawning. No attachment surface other than the first membrane of the egg develops. The eggs become fused, apparently by their own membranes, to the special setae in the brood pouch of the female. Egg stalks are drawn out by stretching movements of the pleopods. It is possible that the membrane is activated to become adhesive by the secretion of an enzymelike material released among the eggs by the mother from the pleopodal glands during attachment. Only near sources of this secretion would such attachment occur; therefore, the eggs usually do not stick to each other but rather to the setae.

Since the early 1930's much experimental work has been done on the endocrine system in relation to color control in *Palaemonetes* assumed to be *vulgaris*. The shrimp has been found to have four kinds of pigment under independent hormonal control—red, yellow, white, and blue. These pigments are mediated through the eyes by the background on which the animal is found. The source of the hormones is principally the sinus gland in the eyestalk and the central nervous organs (Brown, 1933, 1935a, 1935b, 1948; Brown, Fingerman, and Hines, 1952; Brown, Hines, and Fingerman, 1952; Brown, Webb, and Sandeen, 1952). Persons interested are referred to the source material, for the conclusions are too detailed for adequate summary here.

Palaemonetes (Palaemonetes) intermedius Holthuis

Figure 48

Palaemonetes (Palaemonetes) intermedius Holthuis, 1949, p. 94, fig. 2, j–l.—Holthuis, 1952, p. 241, pl. 55, figs. a–f (rev.).

Recognition characters.—Rostrum reaching to or somewhat beyond end of antennal scale, tip directed upward making upper margin more or less concave; upper margin with 7 to 10 (usually 8 or 9) teeth, first tooth placed behind orbital margin, second tooth before or just over posterior orbital margin; teeth rather evenly divided over

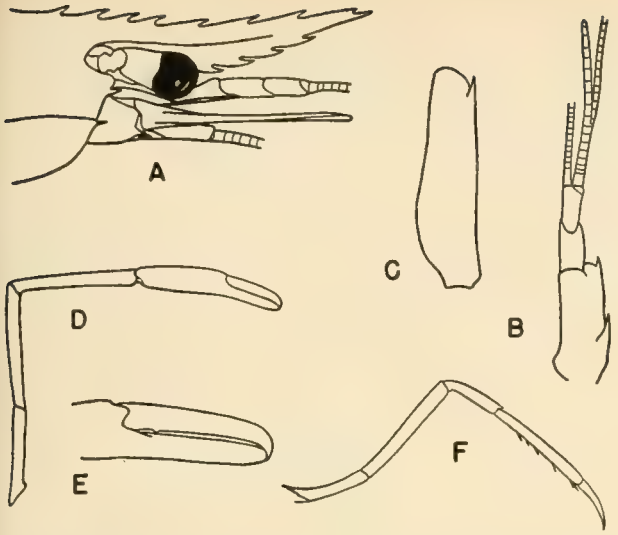

FIGURE 48.—*Palaemonetes (Palaemonetes) intermedius* Holthuis. A, anterior part of body in lateral view; B, antennule; C, antennal scale; D, second leg of female; E, fingers of second leg of female; F, third leg; A–F × 4.75 (after Holthuis, 1952).

dorsal margin up to often bifurcate tip, distal teeth more widely spaced than proximals; lower margin with 4 or 5 (occasionally 3) teeth. Carapace smooth; antennal spine present; branchiostegal spine on anterior margin just below branchiostegal groove. Eyes well developed. Antennular peduncle as in *vulgaris*, basal article with slender stylocerite reaching about to middle of article, anterolateral spine of article strong, overreaching rounded anterior margin; upper antennular flagellum with both rami fused for 7 to 10 joints; free part of shorter ramus with 7 to 12 joints, longer than fused portion. Antennal scale slender, 3 to nearly 4 times as long as broad in females, even more slender in males; outer margin straight or slightly concave; terminal tooth reaching about to end of lamella.

First legs almost reaching tip of antennal scale; fingers as long as palm; carpus twice length of chela and slightly longer than merus. Second legs in adult female usually with almost entire chela reaching beyond antennal scale; fingers a little over half length of palm, cutting edge of dactyl with one proximal tooth, remainder of cutting edges of both fingers entire; carpus 1.2 to 1.5 times length of palm and as long as merus. Second leg of male somewhat more slender than in female; only fingers reaching beyond scale; carpus as long as merus. Third leg with propodus less than twice as long as carpus. Fifth leg with propodus about three times as long as dactyl, twice as long as carpus.

Abdomen smooth; pleura of fifth segment with tip rectangular or slightly acute; sixth segment 1.5 times length of fifth, somewhat shorter than telson. Telson with two pairs of dorsal spines; anterior pair somewhat behind middle; second pair halfway between these and tip; posterior margin with strong median point flanked by two pairs of spines, inner pair longest and between these, two feathered setae. Outer margin of uropodal exopod with a strong terminal tooth flanked by a slender movable spine medially.

Measurements.—Length of body: male, 30 mm.; ovigerous females, 20 to 42 mm.

Variations.—In males and juveniles, the legs reach less far forward than in ovigerous females (Holthuis, 1952). The second chelae of some females have one tooth on the cutting edge of each finger.

Color.—Transparent in life.

Habitat.—Estuarine waters, especially in beds of submerged vegetation.

Type locality.—Iron Box Bay, Chincoteague Bay, Va.

Known range.—Long Island, N.Y., to Port Aransas, Tex. (from specimens examined by Holthuis, 1952). Literature records: Vineyard Sound to Aransas National Wildlife Refuge, Tex. (Holthuis, 1952).

Remarks.—The confused taxonomic status of this species in literature is discussed in the account for *P. vulgaris* and dealt with in more detail by Holthuis (1952). Ovigerous females have been found from February to April in Texas (Hedgpeth, 1950), and from May to September in Virginia and the Carolinas.

Palaemonetes (Palaemonetes) pugio Holthuis

Figure 49

Palaemonetes vulgaris: Hay and Shore, 1918, p. 393, pl. 27, fig. 5.

Palaemonetes (Palaemonetes) pugio Holthuis, 1949, p. 95, figs. 2, m–o.—Holthuis, 1952, p. 244, pl. 55, figs. g–l (rev.).

Recognition characters.—Rostrum reaching to or slightly beyond end of antennal scale; straight, sometimes slightly upturned at tip; dorsal margin with 7 to 10 (usually 8 or 9) teeth, distal teeth more widely spaced than proximal teeth, first

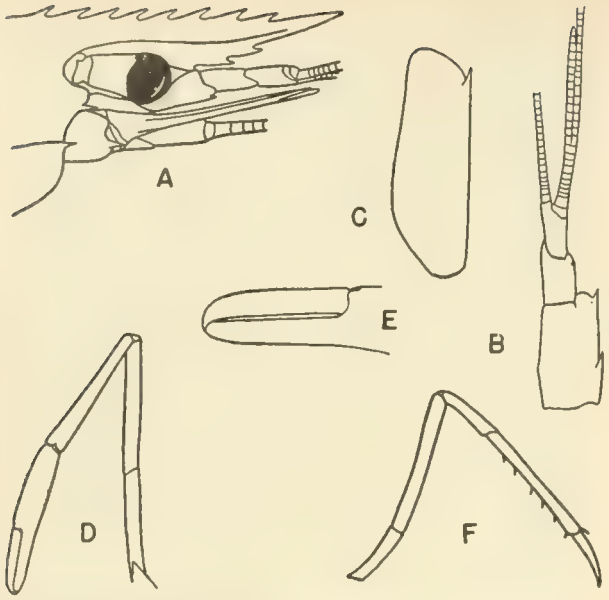

FIGURE 49. *Palaemonetes* (*Palaemonetes*) *pugio* Holthuis. A, anterior part of body in lateral view; B, antennule; C, antennal scale; D, second leg of female; E, fingers of second leg of female; F, third leg; A–F × 4.75 (after Holthuis, 1952).

tooth placed behind orbital margin, distal tooth placed at a distance from tip leaving space before tip unarmed; lower margin with 2 to 4 (usually 3) teeth, distal tooth also placed at distance from tip, tip dagger shaped. Carapace smooth; antennal spine present; branchiostegal spine on anterior margin just below branchiostegal groove. Eyes well developed. Antennular peduncle as in *vulgaris*; basal article with slender stylocerite reaching slightly beyond middle of article, anterolateral spine of article strong, overreaching rounded anterior margin; upper antennular flagellum with both rami fused for 10 to 14 joints; free part of shorter ramus with 12 to 18 joints, longer than fused portion. Antennal scale 2.5 to 3 times longer than broad (length 3 times breadth in males); outer margin convex; terminal tooth strong, almost reaching end of lamella.

First legs not quite reaching tip of antennal scale; fingers as long as palm; carpus nearly twice length of chela and slightly longer than merus. Second legs stronger than first; in adult female, fingers reaching beyond scale, fingers more than half length of palm, cutting edges of both fingers with no teeth, often gaping proximally; carpus 1.3–1.5 times length of palm but shorter than entire chela; merus as long as carpus. Male with second legs more slender and shorter than in female; fingers shorter than palm; carpus nearly as long as whole chela and as long as merus. Third legs with propodus twice length of carpus. Fifth leg with propodus about 2 times length of dactyl, 2.5 times as long as carpus.

Abdomen smooth; fifth abdominal segment with pleura ending in an acute tooth, sometimes extremely small; sixth segment half again as long as fifth, somewhat shorter than telson. Telson with two pairs of dorsal spines; anterior pair somewhat behind middle; second pair halfway between these and tip; posterior margin with strong median point flanked by two pairs of spines, inner pair longest, and between them two feathered setae. Outer margin of uropodal exopod with a strong terminal tooth flanked by a slender movable spine medially.

Measurements.—Length of body: male, 33 mm.; ovigerous females, 30 to 50 mm.

Variations.—Males differ from females as follows: smaller size, more slender rostrum, free part of shorter ramus of upper antennular flagellum longer in relation to fused part, somewhat shorter legs, and carpus of second leg longer in relation to chela. Young individuals resemble males (Holthuis, 1952). The second chelae of a few females have one small tooth on the cutting edge of the dactyl.

Color.—Transparent in life.

Habitat.—Estuarine waters, especially in beds of submerged vegetation.

Type locality.—Lagoon near Cove Point Light, Chesapeake Bay.

Known range.—Essex County, Mass., to Port Aransas, Tex. (from specimens examined by Holthuis, 1952). Literature records: Cold Spring Harbor, Long Island, N.Y., to Corpus Christi, Tex.

Remarks.—The confused taxonomic status of this species in literature is discussed in the account for *P. vulgaris* and dealt with in more detail by Holthuis (1952).

Broad (1957a) worked out the larval development of *P. pugio* and *P. vulgaris*. He found mature individuals of both species were abundant in the Beaufort, N.C., area from April until mid-

October. Larval development of the 2 species is similar, and 10 zoeal stages and a postlarval stage were described for both. The chief difference between larvae of the two species is in the presence of a pair of chromatophores found on the second abdominal sternite of *P. pugio* but lacking in *P. vulgaris*. The number of larval stages and length of the developmental period may vary, and such variation is apparently due to availability of suitable food. In rearing *Palaemonetes* with artificial diets, Broad (1957b) found that algae alone were not sufficient to promote survival; mixtures of plant and animal food were better, but best survival was obtained by feeding living *Artemia* nauplii. Frequency of molting and rate of development were directly correlated with amount of suitable food available.

Responses of the white chromatophores of *P. pugio* to light and temperature have been investigated by Fingerman and Tinkle (1956). The tendency of white pigment to disperse in bright light, especially on a white background, is normally antagonized by a tendency of the pigment to concentrate with increased temperature. This mechanism is interpreted as maintaining a steady state of white chromatophores in nature.

Pearse (1952b) reported *Probopyrus pandicola* (Parkard) from the gill chamber of this species in Texas.

Family **Gnathophyllidae**

Caridea with first two pairs of legs chelate, first pair smaller than second; carpus of second pair not subdivided. Rostrum short and toothed. Third article of third maxillipeds very broad. Mandibles simple. Second maxillipeds with short seventh article. The family contains but a single genus (Hay and Shore, 1918).

Genus ***Gnathophyllum*** Latreille, 1819

Armstrong, 1940, p. 6 (rev.).—Hemming, 1958b, p. 156.

Gnathophyllum modestum Hay

Figure 50

Gnathophyllum modestum Hay, 1917, p. 72.—Hay and Shore, 1918, p. 395, pl. 28, fig. 1.—Manning, 1963, p. 48, figs. 1–2.

Recognition characters.—Body short and thick; carapace with a moderate carina continuous in front with rostrum and extending about two-thirds of distance to posterior margin. Rostrum

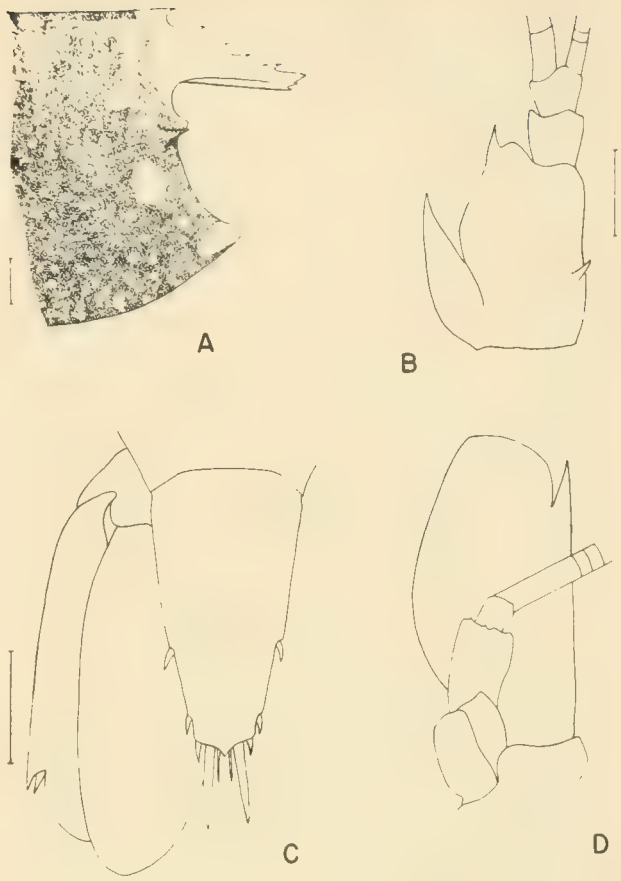

FIGURE 50.—*Gnathophyllum modestum* Hay. A, anterior portion of carapace, lateral view; B, antennular peduncle, ventral view; C, telson and left uropod; D, antennal scale; 1 mm. indicated. B and D to same scale (after Manning, 1963).

obliquely truncate dorsally and armed with five or six dorsal teeth; one or two small ventral teeth near tip; tip reaching to distal end of basal article of antennule. Suborbital angle prominent; antennal spine present; anterolateral angle strongly produced. Eyes rather large and with a prominent, conical, black protuberance on cornea. Antennular peduncles with basal article large, stylocerite reaching beyond middle of article, a spine at anterolateral corner of article; second article with a similar but smaller and blunter anterolateral spine; second and third articles of about equal length; outer antennular flagellum bifurcate, upper ramus longer and thinner than lower ramus. Antennal scale reaching beyond antennular peduncles, lateral margin almost

straight, terminating in a spine, lamella of scale rounded distally, slightly exceeding spine.

Third maxillipeds with merus and carpus broad, closing whole front of buccal region; two terminal articles flattened, much more slender, and extended straight forward. Second pair of legs much stronger than first, exceeding rostrum by length of chela; fingers more than half length of palm. Last three pairs of legs with dactyls bifurcate.

Abdomen with last three segments abruptly smaller than preceding segments and strongly flexed. Telson with a pair of marginal spines at about distal third and a minute pair near tip, tip with median point and with three pairs of spines, intermediate pair longest.

Measurements.—Length of ovigerous holotypic female, 21 mm.

Color.—Body deep brown with many scattered small yellow and a few larger orange spots; antennal scale, distal portions of rostrum and tail fan clear; orbital margins and eyestalks white; legs grading from brown proximally through purple to white distally but barred with purple on distal portion of some elements; markings of yellow below and on some articles of appendages (Manning, 1963).

Habitat.—Found around clumps of coral and sponges in shallow water; to 15 fathoms.

Type locality.—Beaufort, N.C.

Known range.—Beaufort, N.C.; Biscayne Bay, Fla.

Remarks.—This species, long known only from Hay's type specimen, has recently been reported from Florida (Manning, 1963). Manning reviewed the east American species of *Gnathophyllum*, pointing out the close similarity of *G. modestum* to the eastern Atlantic species *G. elegans*, and giving detail on the importance of color patterns in living material as diagnostic characters in the genus. Excellent figures accompany Manning's discussion.

Ovigerous females are known from Florida in June. The date of collection for Hay's specimen is unknown.

Family Alpheidae

Carapace smooth, with cardiac grooves; rostrum reduced; antennal and branchiostegal spines always absent; carapace almost always projecting over eyes (*Automate* excepted). Antennular base cylindrical, basal article not longer than sum of other two articles. Antennal scale rarely longer than antennal peduncle. Mandible bipartite with palp of two points. Chela of first leg predominant, always large (usually asymmetrical); carpus short. Second legs weakly developed; carpus multiarticulate. Third to fifth legs with spinous propodi and simple or bifurcate dactyls; propodus of fifth leg with more or less well-developed brush of bristles in transverse to oblique rows. Abdomen usually with gradual curve, no pronounced bend at third segment; sixth segment short, broad, sexually dimorphic. (Adapted from Banner, 1953).

The biology of snapping shrimp occurring on the east coast of the United States has been reviewed by Knowlton (1960) and the reader is referred to this unpublished but useful work for more complete information than is included here.

KEY TO GENERA IN THE CAROLINAS

a. Eyestalks completely exposed
Automate kingsleyi (p. 62).

aa. Eyestalks covered by carapace.

b. Epipods present on at least first two pairs of legs
Alpheus (p. 63).

bb. Legs without epipods_____*Synalpheus* (p. 69).

Genus *Automate* de Man, 1887

Man, J. G. de, 1887, p. 529.

Automate kingsleyi Hay

Figure 51

Automate kingsleyi Hay, 1917, p. 72.—Hay and Shore, 1918, p. 387, text-fig. 10; pl. 26, fig. 7.

Recognition characters.—Carapace about half length of abdomen; subcylindrical; deeply emarginate dorsally behind eyestalks with rostrum a small median projection; anterior margin entire, produced farthest forward at base of antennular and antennal peduncles. Eyestalks contiguous, broad at base; cornea well developed with a minute point on anterior surface in lateral view. Antennular and antennal peduncles long; stylocerite scalelike, reaching to end of basal antennular article; second antennular article nearly equal in length to first; third very short. Antennal scale extending to middle of terminal article of antennal peduncle; lateral border ending in a small spine; lamella broadly rounded distally, equaling spine. Third maxilliped exceeding an-

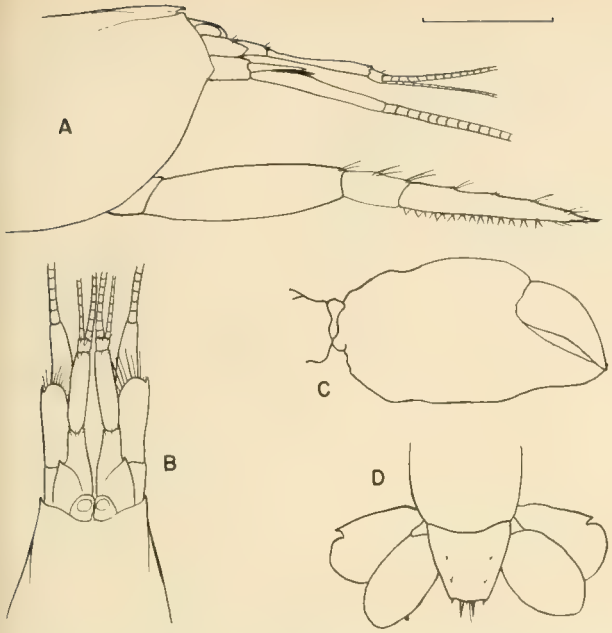

FIGURE 51.—*Automate kingsleyi* Hay. A, anterior part of ovigerous female in lateral view; B, anterior part of body in dorsal view; C, large chela; D, uropods and telson in dorsal view; 1 mm. indicated (C after Hay and Shore, 1918).

tennal peduncle by less than length of terminal article.

First pair of legs chelate, prismatic, unequal; larger one appearing somewhat rougher and stouter than smaller one; fingers slightly gaping, immovable finger in line with hand and broad at base; dactyl narrower and moderately curved; carpus short; merus nearly as long as dactyl. Second pair of legs nearly as long as first but slender, weakly chelate, and with carpus divided into five joints with proportions of 1 : 1.25 : 0.80 : 0.66 : 0.80. Third to fifth legs with dactyls simple.

Abdomen well developed; compressed; with strong pleopods. Telson tapering; truncate terminally, ending in two short lateral spines flanked medially by two longer spines and a median pair of feathered setae; dorsally armed with two pairs of spines, first pair at midlength, second at three-fourths length. Uropods with oval blades; lateral border of exopod deeply notched distally, border ending in a small tooth flanked medially by a strong movable spine.

Measurements.—Length of body: ovigerous females, 7 to 16 mm.

Color.—Almost transparent except for a small amount of red pigment on appendages and telson.

Habitat.—Unknown.

Type locality.—Shark Shoal breakwater, near Beaufort Inlet, N.C.

Known range.—Known only from and near type locality, and from Pelican Island, English Harbor, Barbados (Schmitt, 1924a).

Remarks.—Aside from the Barbados specimen, only three specimens from the Beaufort, N.C., area are known. The ovigerous type was taken July 9, 1916, and another ovigerous female on September 7, 1960. The third specimen is immature. Hay and Shore (1918) reported that the type remained alive in the laboratory for over a month, during which time the eggs dropped off and the specimen molted twice without appreciably increasing in size.

Genus *Alpheus* Fabricius, 1798

Banner, 1953, p. 46.—Hemming, 1958b, p. 108.

The status of the name *Alpheus* (and its confusion in usage with the name *Crangon*, at least among American workers during the first half of this century) was in doubt until nomenclatural stability was effected by the International Commission on Zoological Nomenclature (Opinion 334). The Official List of Generic Names in Zoology (Hemming, 1958b) now lists *Alpheus* Fabricius, 1798, as the correct generic name for the species here considered, and the Official Index of Rejected and Invalid Generic Names in Zoology (Hemming, 1958a) lists the suppressed generic names *Alpheus* Weber, 1795, and *Crangon* Weber, 1795, formerly applied to the species here considered.

KEY TO SPECIES IN THE CAROLINAS

a. Orbital hoods of carapace with a small spine in front ..... *formosus* (p. 64).

aa. Orbital hoods of carapace without a distinct spine.

b. Orbital hoods forming an anterior toothlike projection; large hand with a groove above and below along outer margin and between these grooves a thick tooth ..... *normanni* (p. 65).

bb. Orbital hoods rounded anteriorly; large hand broad and notched on both margins.

c. Base of rostrum passing gradually into lateral dorsal surface ..... *heterochaelis* (p. 66).

cc. Base of rostrum with borders sharply defined ..... *armillatus* (p. 67).

Alpheus formosus Gibbes. Striped snapping shrimp

Figure 52

Alpheus formosus Gibbes, 1850, p. 196.—Verrill, 1922, p. 84, text-figs. 5d, 6a; pl. 20, fig. 3; pl. 23, figs. 5 a, b; pl. 29, figs. 4, a–u; pl. 25, figs. 6–6a.

Crangon formosus: Hay and Shore, 1918, p. 384, pl. 26, fig. 5.—Schmitt, 1935a, p. 144.

Recognition characters.—Rostrum beginning at posterior line of eyes and reaching about to second article of antennular peduncle; flat above; margins concave at base but regularly convergent anteriorly and with scattered stiff hairs; tip rounded, often bearing two or three minute spines. Carapace half length of abdomen, compressed, not grooved; orbital hoods each with an acute, anteriorly directed spine much shorter than rostrum; anterior margin emarginate below orbital hoods. Eyes completely covered by carapace. Antennular peduncles with scalelike stylocerite, slender tip reaching slightly beyond basal article; second article twice length of third; inner flagellum filiform, outer flagellum thick proximally, filiform distally. Antenna longer than body; antennal scale with strong apical spine reaching to or beyond tip of antennular peduncle, spine separated from and exceeding lamella; a weak spine (basicerite) below near base of scale. Third maxillipeds with terminal joint hairy; slightly exceeding antennal peduncle.

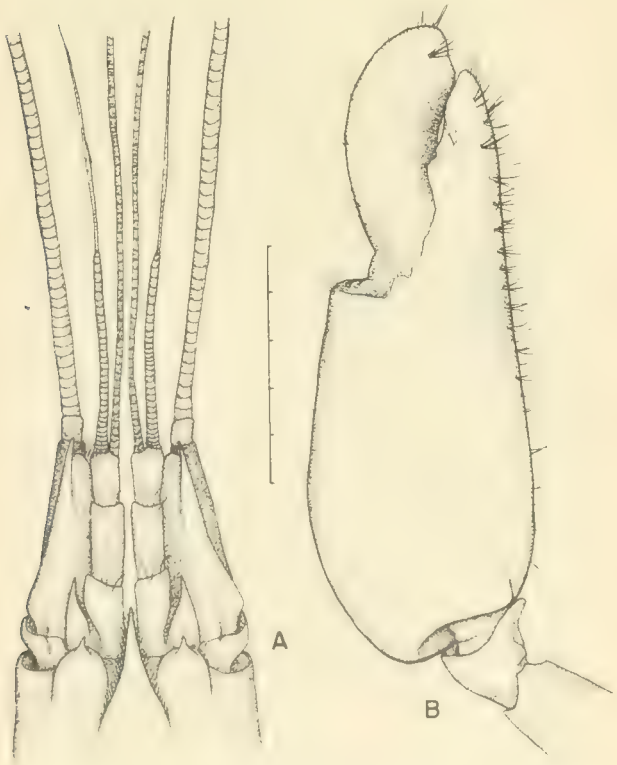

FIGURE 52.—*Alpheus formosus* Gibbes. A, anterior part of body in dorsal view; B, outer surface of large chela; 5 mm. indicated.

First legs strongly chelate, very unequal. Larger leg compressed, smooth above and unnotched along margins; immovable finger acute, incurved at tip, shorter than stout and gradually arched, blunt dactyl; carpus short, convex above, with a distal tooth; merus with an acute distal spine. Smaller chela much more slender, long, and smooth, inner surface with a stout spine overhanging base of dactyl; immovable finger nearly straight, slender, somewhat turned up near tip; dactyl about half length of hand, nearly straight to about middle, then gently arched to tip, hairs arising from a nearly straight groove below ridge on both sides; inner surfaces of fingers with a slender groove and carina; fingers shutting closely. Second pair of legs slender; weakly chelate; carpus subdivided, with joints diminishing in length as follows (numbered from proximal end): 1, 5, 2, 3–4. Third to fifth legs with simple dactyls.

Telson with two pairs of dorsal spines at about one-third and two-thirds length; posterolateral corners with a pair of spines, medial spine much longer than lateral, distal margin with long hairs. Uropodal exopods with lateral margin ending in a black movable spine between two fixed spines; black spine remaining amber colored after long preservation.

Measurements.—Length of body: ovigerous females, 17 to 35 mm.

Color.—Color pattern conspicuous and characteristic; ground color yellowish or greenish brown finely speckled with orange; a narrow light stripe along middorsal line extending from distal end of antennular peduncle to base of telson, line light orange anteriorly merging into yellowish green and finally gray posteriorly, a brown stripe on each side dorsolaterally and below this another stripe of white, or colors similar to dorsal stripe, along each side followed by a stripe of light reddish brown and still another stripe of blue bordering abdomen; chelae greenish brown with orange red fingers; antennules, antennae, and walking

legs blue; telson and uropods white at base blotched and bordered with yellow.

Habitat.—Lives in holes and crevices in shell bars, stones, and dead corals; water's edge to 23 fathoms.

Type locality.—Key West, Fla.

Known range.—Near Beaufort, N.C., through West Indies to Santos, São Paulo, Brazil; Bermuda.

Remarks.—Ovigerous females have been taken off Venezuela in April, Beaufort, N.C., in July, Bimini in October, and Santos, Brazil, in June. Manter (1934) found metacercariae of *Helicometrina nimia* encysted in muscles of *A. formosus* at Tortugas.

Alpheus normanni Kingsley. Green snapping shrimp

Figure 53

Alpheus affinis Kingsley, 1878a, p. 195.
Alpheus normanni Kingsley, 1878b, p. 93.
Alpheus packardii Kingsley, 1880, p. 417.—Verrill, 1922, p. 80, pl. 20, figs. 2–5; pl. 21, fig. 5; pl. 22, fig. 7; pl. 23, figs. 6, c–d; pl. 25, figs. 4, a, b; pl. 31, figs. 1, b–l, 2, b–u, 3, u, t (rev.).
Crangon packardii: Hay and Shore, 1918, p. 385, pl. 26, fig. 4.—Schmitt, 1035a, p. 144.

Recognition characters.—Rostrum with carina extending as far back as base of eyestalks, spiniform tip not reaching to base of second article of antennule. Carapace about two-thirds length of abdomen, somewhat compressed; cervical groove hardly evident; front with ocular hoods produced into an obtuse angle above each eye; anterior margin emarginate below ocular hoods. Eyes well developed but completely covered by carapace. Stylocerite scalelike with spiniform tip reaching about to end of basal article of antennule; third article much shorter than second; inner antennular flagellum slender, outer one shorter with proximal four-fifths enlarged. Antennae a little longer than body, slender; antennal scale reaching a little beyond end of antennular peduncle, lateral margin slightly sinuous with strong terminal spine separated from and exceeding lamella; a strong ventral spine (basicerite) near base of scale. Third maxillipeds slender, not reaching tip of antennal scale; terminal article with long hairs.

First legs strongly developed with chelae unequal. Larger leg broad and flattened; slightly sinuate along inner margin; outer margin with a longitudinal groove above and below, a ridge

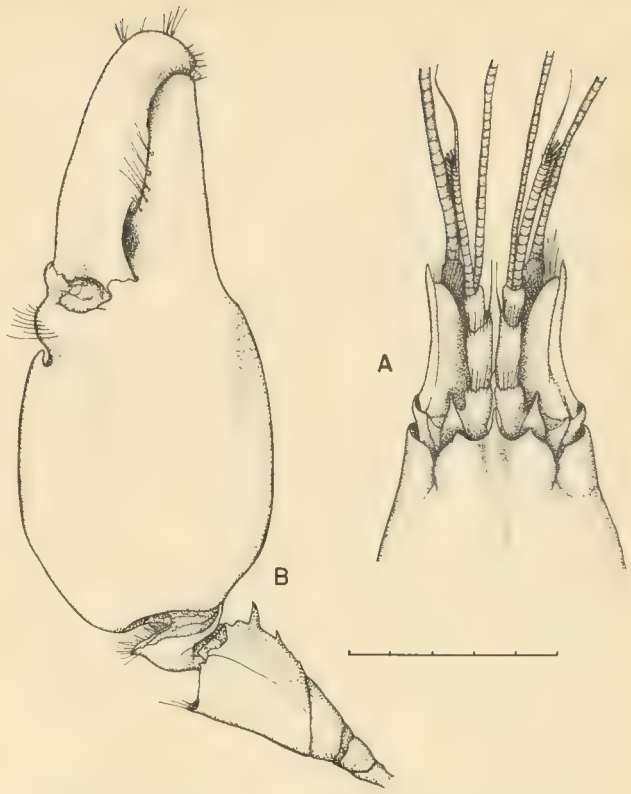

FIGURE 53.—*Alpheus normanni* Kingsley. A, anterior portion of body in dorsal view; B, large chela in ventrolateral view; 5 mm. indicated.

between grooves ending in a strong tooth behind base of dactyl; dactyl heavy, curved, toothed at base. Smaller chela about half as wide and three-fourths as long as larger one; similarly formed but with a sharp spine above (and a small one below in males) at base of dactyl; no basal tooth on dactyl; sexually dimorphic fingers in males broad externally but with keeled, closely fitting opposed edges fringed by dense hairs; females with hand a bit hairy but fingers unornamented; carpus of both legs short, broad, irregularly cup shaped, merus with a spiniform tooth near distal end and one or two spines below, distal end cupped to receive carpus with leg extended. Second legs very slender, weakly chelate; with carpus subdivided, joints diminishing in length as follows (numbered from proximal end): 2, 1, 5, 3–4. Third to fifth legs with dactyls simple.

Abdomen somewhat compressed. Telson with sides slightly convergent distally; two pairs of dorsal spines, first pair at one-third, second at

two-thirds length; tip broadly rounded, a pair of spines at each posterolateral corner, distal margin heavily setose; a pair of anal tubercles beneath with accompanying cups on uropods forming locking devices. Uropods oval; exopod with lateral margin ending in a small spine flanked medially by a strong movable tooth.

Measurements.—Length of body: male, 26 mm.; ovigerous female, 16 mm.

Color.—Gray or dull green, sometimes with a median and lateral stripe of whitish often clouded or mottled with dark green or brown, a paler spot behind each eye; large chela dark green usually banded with yellowish brown or yellow on inner surface; smaller chela and other legs paler, often banded with dull gray or reddish; occasionally body banded with red and pale yellow, large chela with two pale bands, immovable finger blackish, dactyl reddish (various authors).

Habitat.—Shelly or rocky bottoms, in burrows in sand or on pilings in shallow water; common in saltier portions of estuaries; water's edge to 40 fathoms.

Type locality.—Key West, Fla.

Known range.—North Carolina through West Indies to Barbados, Curaçao, and Aruba; Alligator Harbor, Fla., to Sabine, Tex.; Bermuda; Sonora, Mexico(?).

Remarks.—This is one of the commonest snapping shrimps in the Beaufort, N.C., region. As Hay and Shore (1918) pointed out, this was probably the species called *Alpheus minor* in early lists for the area. The latter species is correctly referred to *Synalpheus minus* (Say) and is found only in offshore waters, a different habitat from that frequented by *Alpheus normanni*. Brooks and Herrick (1892) followed the older lists in calling this species *Alpheus minor* (*minus*) and illustrated the adult in color on plate 1 and larval stages on plates 16 and 17. They illustrated the first three larval stages, as well as stages in segmentation of the embryo, but their specific identifications are somewhat unreliable.

Ovigerous females have been taken through much of the annual cycle in various localities: January and March, Cuba; June, Louisiana; August, Bermuda, Louisiana, Mississippi; April to September in the Carolinas; November and December, Puerto Rico.

Alpheus heterochaelis Say. Big-clawed snapping shrimp

Figure 54

Alpheus heterochaelis Say, 1818, p. 243.—Verrill, 1922, p. 76, pl. 22, figs. 1, 2, 4, a–c; pl. 24, figs. 7, 7a; pl. 30, figs. 1–1a, 1t, 2a–2e; pl. 33, figs. 1 ,2 (rev.).

Crangon heterochaelis: Hay and Shore, 1918, p. 386, text-fig. 8, pl. 26, fig. 6.—Schmitt, 1935a, p. 144.

Recognition characters.—Rostrum carinate, extending back about as far as base of eyestalks; tip not reaching to base of second article of antennular peduncle. Carapace more than half length of abdomen, somewhat compressed; without grooves; front produced into a rounded ocular hood over each eye; rostro-orbital depressions passing gradually into dorsal surface; emarginate below eye on anterior border. Eyes relatively small, covered by carapace. Antennular peduncles with scalelike stylocerite, minute spine at tip not reaching end of basal article; second article twice length of third; inner flagellum filiform, about half length of antenna; outer flagellum with proximal two-thirds thickened. Antennae a little longer than body; antennal scale with strong apical spine reaching slightly beyond antennular

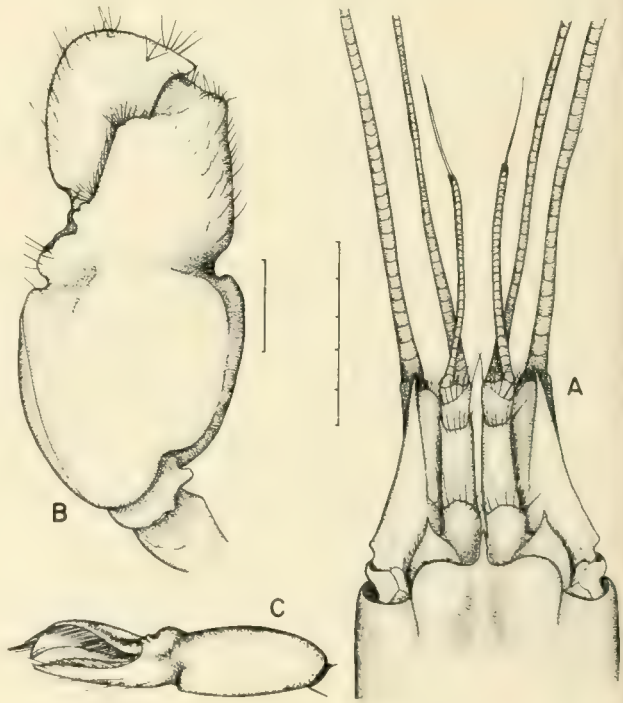

FIGURE 54.—*Alpheus heterochaelis* Say. A, anterior portion of body in dorsal view, 5 mm. indicated; B, large chela in dorsal view, 5 mm. indicated; C, small chela of male (after Verrill, 1922).

peduncle, spine separated from and slightly exceeding lamella; a weak spine (basicerite) below near base of scale. Third maxillipeds with terminal article hairy; slightly exceeding antennal peduncle.

First legs strongly chelate, very unequal. Larger chela thick; outer and inner margins deeply notched near base of fingers; upper and lower surfaces with irregular shallow grooves; dactyl broad, heavy, strongly curved, with large basal tooth. Small chela sexually dimorphic; in male broad, elongate; proximal dorsal area of palm bounded by an impressed line, upper margin notched distally; dactyl flattened and expanded on outer surface; opposed edges of fingers keeled, closely fitting, fringed by dense hairs. Fingers of small chela in both sexes weaker, less curved, and more hairy than in large chela; carpus short; merus smooth. Second legs slender, weakly chelate; carpus subdivided with joints diminishing in length as follows (numbered from proximal end): 1, 2, 5, 4, 3. Third to fifth legs with simple dactyls.

Abdomen compressed, smooth, tapering. Telson with subparallel sides and rounded tip; dorsal surface with two pairs of movable spines, first pair at about midlength, second at a little less than three-fourths length; a pair of spines at each posterolateral corner, medial spine longest; distal margin heavily setose, a pair of anal tubercles beneath with accompanying cups on uropods forming locking devices. Uropodal exopods with lateral border ending in a fixed spine flanked medially by a longer movable spine.

Measurements.—Length of body: male, 40 mm.; female, 50 mm.

Color.—Dark translucent green, slightly flushed with purple on sides of carapace; white markings on chelipeds; walking legs pale red; tips of uropods blue with narrow border of orange on distal margin, outer blade with patch of red just above blue, and a narrow white border; articular surfaces and joints of abdominal segments, and a small streak along cervical groove, white.

Habitat.—Lives among broken shells and stones or in burrows in mud among shells; water's edge to 16 fathoms.

Type locality.—Amelia Island, Nassau County, Fla. (Holthuis, 1959, restr.).

Known range.—Near Hatteras, N.C., to Aransas County, Tex.; Colon, Panama; through West Indies to Iguape, São Paulo, Brazil; Bermuda (Holthuis, 1956).

Remarks.—Brooks and Herrick (1892) gave a good colored figure of this species (plate 2), as well as a series of figures of segmenting eggs and developing larval stages. Because the material they studied originated from both North Carolina and the Bahamas, there is some doubt as to its identity, but a total of four larval stages were illustrated.

This is the largest snapping shrimp found in the Carolinas. It is nearly as abundant as *A. normanni.*

Ovigerous females have been taken through much of the annual cycle in various localities: February and April in Surinam (Holthuis, 1959); March in Panama and Texas; April and May in Louisiana and Florida; July in North Carolina; August and September on the Gulf Coast; October to January in Cuba, Puerto Rico, and Bonaire.

Alpheus armillatus Milne Edwards. Banded snapping shrimp

Figure 55

Alpheus armillatus H. Milne Edwards, 1837, p. 354.—Verrill, 1922, p. 73, text-figs. 5a, 6b; pl. 20, fig. 4b; pl. 21, figs. 4, 4a; pl. 26, figs. 1–1d; pl. 23, fig. 4; pl. 27, figs. 1–1s (rev.).

Crangon armillatus: Hay and Shore, 1918, p. 386, text-fig. 9; pl. 27, fig. 1. Schmitt 1935a, p. 142.

Recognition characters.—Rostrum in form of a narrow raised crest from base to tip, projecting beyond orbital hoods, widening abruptly just behind eyes into a triangular area with borders slightly concave and distinctly limiting rostro-orbital depressions, slightly overhanging depressions in adult specimens. Carapace compressed; orbital hoods prominent in front with a slight obtuse anterior lobe, but without spine or denticle, and with a strong emargination below eyes. Eyes entirely covered by carapace. Antennules with stylocerite large, scalelike, not very acute, and not reaching to end of basal antennular article; second article longer than third; inner flagellum filiform; outer flagellum thickened in about proximal half. Antennal scale with a strong terminal spine equal to or extending beyond antennal peduncle, scale distinctly curved outward in distal two-thirds; a small spine (basicerite) near base of scale. Third

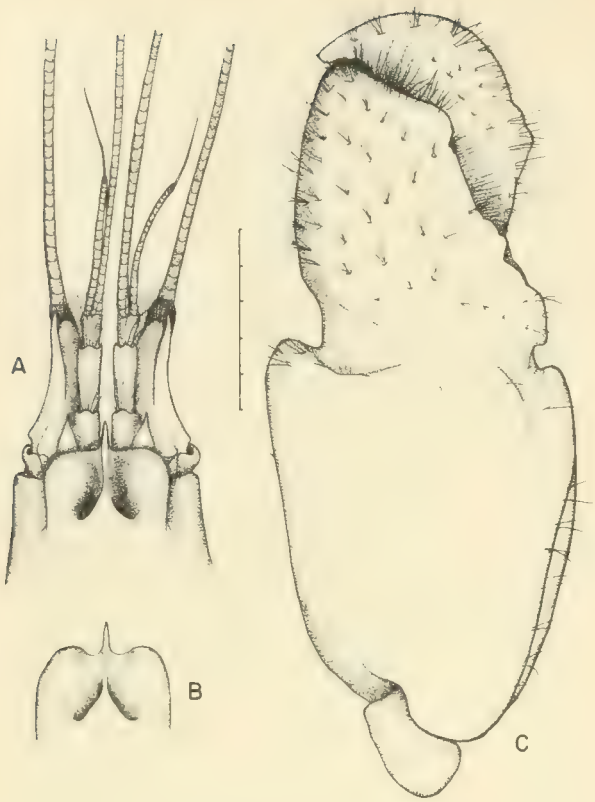

FIGURE 55.—*Alpheus armillatus* Milne Edwards. A, anterior portion of body in dorsal view; B, rostral region in dorsal view with light showing from posterior; C, large chela in dorsal view; A–C, 5 mm. indicated.

maxilliped covered with long hairs distally, reaching about to end of antennal peduncle.

First legs strongly chelate, hairy, unequal. Larger chela thick; outer and inner margin deeply notched near base of fingers; upper and lower surfaces with irregular shallow grooves; dactyl broad, heavy, curved, with large basal tooth. Small chela slender; cutting edges of fingers closely fitting, dactyl with a small tooth at base, dactyl in males lacking setose crests and expanded external surface characteristic of *A. heterochaelis*. Second legs long, slender, weakly chelate, with part of merus reaching beyond rostrum; carpus subdivided with joints diminishing in length as follows (numbered from proximal end): 1, 2, 5, 3–4. Third to fifth legs with simple dactyls.

Abdomen smooth, compressed. Telson with two pairs of dorsal spines, first pair at one-third, second at two-thirds length; sides somewhat convergent distally, tip rounded, with a pair of spines at each posterolateral corner, medial spine twice length of outer spine. Uropodal exopod with outer margin ending in a small spine flanked medially by a larger spine.

Measurements.—Length of body: ovigerous females, 31 to 38 mm.

Color.—Body with dark gray or brown ground color, crossed by nine conspicuous lunate or elliptical spots or bands of translucent white equal in width to intervening dark bands; carapace with three white bands, third one at posterior margin; abdomen with six bands, first blending with last on carapace; abdominal bands usually whiter or more clearly defined than bands on carapace; abdomen often dark green with spots bordered by line of orange; uropods and telson usually with a broad crossband and sometimes tipped with orange; chelae thickly speckled with dark gray, whitish bands above, tipped with pale pink or white; antennal peduncles grayish, flagella and walking legs orange yellow banded with white (Verrill, 1922).

Habitat.—Under rocks and shells or in holes in rocks; shallow water.

Type locality.—West Indies.

Known range.—North Carolina, through West Indies to Cananéia, São Paulo, Brazil; Bermuda (Holthuis, 1956).

Remarks.—This species closely resembles *A. heterochaelis*, its similar sized and (in the Carolinas) much more abundant congener. *Alpheus armillatus* is named for its conspicuously banded body, but in preserved material it can be distinguished from similar species by the distinctive form of the rostrum and from *A. heterochaelis* males by the lack of the specialized dactyl on the small first chela.

The species is rarely taken in the Beaufort region of North Carolina. Hay and Shore (1918) found males and females living in pairs under rocks at Fort Macon. Ovigerous females are known from only the first half of the annual cycle: March, Panama; April, Venezuela; May, Barbados; June, Florida and Brazil; August, Bermuda.

Pearse (1932b) reported encysted larvae of *Rhyncobothrius* in viscera of *A. armillatus*.

Coonfield (1940) observed the chromatophore system of this shrimp in one of the early studies

of this kind, showing that it reacts to different backgrounds under varying light conditions.

Hess (1940, 1941) demonstrated that *A. armillatus* is sensitive to light in many regions of the body, regardless of the amount of time elapsed since the preceding molt. At Tortugas, he found that diurnal molting in this shrimp is apparently controlled by daily temperature changes, molting occurring when the temperature rises to or above 29° C. Animals in constant temperature failed to exhibit diurnal molting as did ovigerous females.

Darby (1934) studied regeneration of chelae in *A. armillatus* and *Synalpheus longicarpus* together with determination of right or left handedness. He found that in development of chelae a stage was reached that permitted determination of which side would have a large chela. Equal chelae were produced experimentally and were of three varieties: (1) both small (pinch claws); (2) both large (snap claws); and (3) both intermediate.

Darby offered an hypothesis, involving two substances and a metabolic condition, which could explain the regenerative phenomena in these and allied crustaceans. In such animals, a substance A is produced which controls production of pinch claws; but at certain stages in the intermolt cycle a substance B is produced, for a limited time, and is concentrated in whichever claw is regenerating or already modified as a snap claw. This circumstance will produce or reinforce production of a snap claw. Chance alone is responsible for whether a snap claw will be on one side or the other, or whether the animal will be symmetrical. Also, time at which regeneration occurs depends on chance.

Genus *Synalpheus* Bate, 1888

Banner, 1953, p. 26.—Hemming, 1958b, p. 161.

KEY TO SPECIES IN THE CAROLINAS

a. Dactyls of third, fourth, and fifth legs with two very unequal hooks, ventral strongest (broadest); an inconspicuous, obtuse supernumerary process proximal to ventral hook_____*fritzmuelleri* subsp. (p. 69).

aa. Dactyls of third to fifth legs with two hooks approximately equal in width at base.

b. Dactyls long and slender, hooks continuing general direction of axis of dactyl; stylocerite longer than basal article of antennular peduncle; lamella of antennal scale present.

c. Frontal teeth more or less equilaterally triangular, at times with concave margins, but never with an inferior vertical prolongation to rostrum; basicerite strongly spinous above *minus* (p. 70).

cc. Frontal teeth always longer than wide, spinous; rostrum armed with a ventral prolongation which embraces ocellary beak; basicerite unarmed above_____*townsendi* (p. 72).

bb. Dactyls short, hooks strongly curved, ventral one usually bent at considerable angle to axis of dactyl; stylocerite not exceeding first article of antennular peduncle; antennal scale lacking lamella in male, small in female_____*longicarpus* (p. 73).

Synalpheus fritzmuelleri Coutiere

Figure 56

Synalpheus fritzmuelleri Coutiere, 1909, p. 35, fig. 18.—Verrill, 1922, p. 97. Schmitt, 1935a, p. 148.

Recognition characters.—Rostrum slender, compressed, acute from dorsal view, a little longer than orbital spines, reaching to midlength of visible portion of basal antennular article. Orbital spines wide at base, acuminate; margins incurved. Eyes completely covered by carapace. Antennular peduncle with stylocerite of basal article reaching

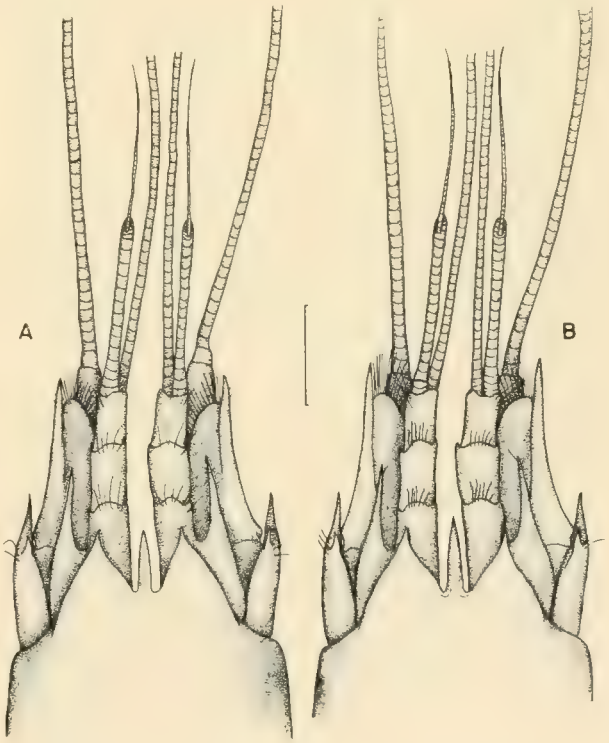

FIGURE 56.—A, *Synalpheus fritzmuelleri* Coutiere, anterior portion of animal in dorsal view; B, *Synalpheus fritzmuelleri elongatus* Coutiere, anterior portion of animal in dorsal view; 1 mm. indicated.

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to middle of second article; third article slightly shorter than second; inner flagellum filiform outer bifurcate beyond about eighth joint, thickened proximally. Spine of antennal scale equaling terminal article of antennal peduncle, both reaching a little beyond antennular peduncle, spine separated from and exceeding narrow lamella distally; basicerite with a short, sharp lateral spine nearly as long as stylocerite; above it a smaller, acute, secondary spine.

First pair of legs chelate, unequal. Large chela ellipsoidal, only a little swollen in middle; a small obtuse tubercle on distal dorsal margin; width of palm about one-third total length of chela; dactyl heavy, strongly arched above; immovable finger narrow at tip; carpus short and wide, prolonged downward and inward; merus stout, superior margin ending distally in a sharp angular point. Smaller chela similar in form; fingers pointed; carpus short, cup shaped; merus like that of larger chela. Second legs slender, weakly chelate; carpus subdivided, first joint about equal to remaining four. Third to fifth legs with bifurcate dactyls, hooks unequal; outer one thinner and a little longer, regularly curved, sharp; inner one wider at base, strongly divergent, curved inward; proximal to inner hook a slight obtuse protuberance or rudimentary spur.

Telson broad, tapering, obtusely rounded distally; each posterior angle with a pair of unequal spines; two pairs of small dorsal spines, first pair at midlength, second at three-fourths length. Uropodal exopods with lateral margin ending in a notch with a fixed spine on each side, a longer movable spine between them.

Measurements.—Length of body: ovigerous female, 22 mm.

Variations.—In the subspecies *S. f. elongatus* Coutiere (1909, p. 37, fig. 19) the lateral spine of the antennal scale greatly exceeds the terminal article of the antennal peduncle, and the rostrum is decidedly longer than the ocular spines. In the subspecies *S. f. carolinensis* Verrill (1922, p. 99, pl. 22, fig. 6; pl. 39, figs. 1-1d) and *S. f. caribaea* Verrill (1922, p. 98, text-fig. 8; pl. 39, figs. 3a-3c) the basicerite is shorter than in typical specimens.

Color.—Synalpheus fritzmuelleri: chela varying shades of green, darker toward extremities of fingers; body more or less colorless, specked with quite numerous tiny red chromatophores. *Synalpheus fritzmuelleri elongatus:* similar to preceding; chelipeds and second legs blue, except anterior part of chela light green (Schmitt, 1930).

Habitat.—Often found living in sponges; low tide mark to 28 fathoms.

Type locality.—Synalpheus fritzmuelleri, Marco, Fla.; *S. f. elongatus*, Mouth of Bull Creek, S.C.

Known range.—Typical *fritzmuelleri:* Nege, Greenland (Stephensen, 1950); off Beaufort, N.C., to Port Aransas, Tex.; West Indies to Curaçao; Old Providence Island; Tres Marias Archipelago, Mexico; Bermuda. Subspecies *elongatus:* off Beaufort, N.C., to Florianopolis, Santa Catarina, Brazil, including Jamaica and Barbados; Tres Marias Archipelago, Mexico. Subspecies *carolinensis:* Fort Macon, N.C. Subspecies *caribaea:* Dominica.

Remarks.—Distribution of the named subspecies and varieties of *Synalpheus fritzmuelleri* shows that modern revisionary work in the Western Atlantic is needed. Until thorough study is made, the various names must be retained, but it is likely that the present designations do not adequately explain local populations which parallel each other at widely separated locations. As Banner (1953) pointed out, earlier workers, with only a few specimens from these widely separated localities, naturally tended to name the variants, the range of variation being then unknown. Varietal names, therefore, must be regarded as conditional. Verrill (1922, p. 89) may have concurred for he quoted Stebbing's dim view of naming infinite variations but proceeded to name varieties anyway.

In the Carolinas, this species lives on offshore reefs (Pearse and Williams, 1951) in large sponges. Specimens may be found in beach drift after severe storms. Ovigerous females of typical *fritzmuelleri* are known from the Carolinas in February, and June to October, indicating a long breeding season. Ovigerous females of *S. f. elongatus* are known from Barbados in May, and North Carolina in June and July.

Synalpheus minus (Say)

Figure 57

Alpheus minus Say, 1818, p. 245.

Synalpheus minus: Hay and Shore, 1918, p. 382, text-fig. 5; pl. 26, fig. 3 (rev.).—Verrill, 1922, p. 102, pl. 21, fig. 1; pl. 23, fig. 3; pl. 25, fig. 3; pl. 31, fig. 4; pl. 33, figs. 4, 4a; pl. 36, figs. 1–1d, 2; pl. 47, figs. 1–1c, 2; pl. 48, figs. 3–3c (rev.).—Schmitt, 1935a, p. 149.

Recognition characters.—Front of carapace with three teeth each in form of equilateral triangle; rostrum usually a little wider at base, compressed and sometimes slightly longer than orbital teeth. Eyes completely covered by large orbital hoods. Basal article of antennular peduncle with stylocerite reaching to distal third of second article; third article half length of second; second of intermediate length; inner flagellum filiform, outer flagellum thickened proximally. Antennal scale narrow, inner edge regularly curved; lateral spine a little longer than antennular peduncle, separated from and exceeding lamella; basicerite reaching to distal end of basal antennular article, above it a prominent secondary spine.

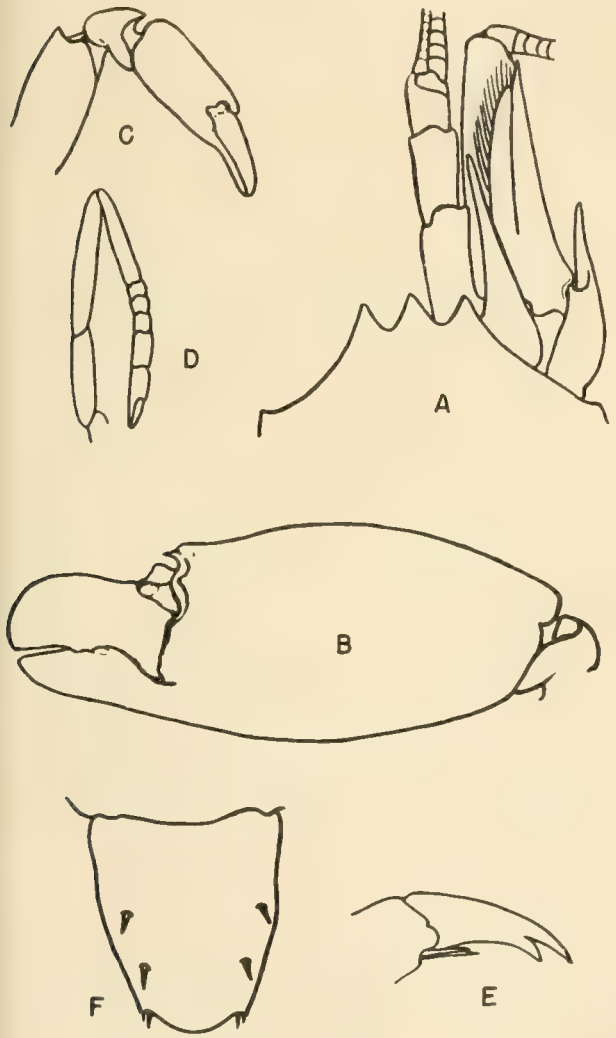

FIGURE 57.—*Synalpheus minus* (Say). A, anterior part of body in dorsal view, with appendages of right side; B, large chela; C, small first cheliped; D, second leg showing subdivided carpus; E, dactyl of third leg; F, telson in dorsal view (after Coutiere, 1909).

First legs chelate, unequal, thicker in male than in female. Large chela ovoid; palm about 2.5 times length of fingers, anterior dorsal margin with a strong, sharp tooth at inner side and a blunter tooth on lateral and ventral side near base of dactyl; dactyl broad, larger than immovable finger, tip obtuse, cutting edge a little sinuous, a large tooth at base, dorsal edge curved distally; immovable finger with tip nearly straight, inner edge a little sinuous. Smaller chela elongate, slender, about one-third length of larger; fingers a little shorter than palm, with tufts of hair, acute at tips and curved a little downward; palm narrowly elliptical, surface plain. Second legs slender, weakly chelate; carpus subdivided with joints diminishing as follows (numbered from proximal end): 1, 5, 2–3–4.

Telson with sides slightly sinuous, tip broadly rounded; two pairs of dorsal spines, first pair at about midlength, second pair at about three-fourths length; distal margin with a pair of spines at each posterolateral corner. Uropodal exopods with lateral margin ending in notch armed with two spines separated by a longer movable spine.

Measurements.—Length of body: female, 35 mm.

Color.—Body translucent, yellowish white; large chela white or translucent gray, fingers orange, tips red; banded near base of fingers with white in female, white tipped with green in male.

Habitat.—Lives in dead corals and commensally in sponges; shallow water to 37 fathoms.

Type locality.—Southern [United] States.

Known range.—Near Cape Hatteras, N.C., through West Indies to Alagoas, Brazil; Bermuda.

Remarks.—A number of authors, among them Hay and Shore (1918) and Verrill (1922), have pointed out that Brooks and Herrick (1892) erroneously called *Alpheus normanni* (=*packardii*) by the name *A. minus* in their profusely illustrated monograph. The true *Synalpheus minus* was not treated by them, however, and, at least in the Beaufort, N.C., area, was not available to them in the harbor area studied.

A long breeding season is indicated for this species. Ovigerous females have been taken from

February to November in various localities from North Carolina to the Gulf coast; in April in Bermuda; and September in Venezuela. Adults usually occur in pairs (Wass, 1955).

Synalpheus townsendi Coutiere. Small snapping shrimp

Figure 58

Synalpheus townsendi Coutiere, 1909, p. 32, figs. 14–17; Hay and Shore, 1918, p. 384, pl. 26, fig. 1 (rev.).—Verill, 1922, p. 100 (rev.).

Recognition characters.—Rostrum slender, 1.5 times as long as lateral teeth and reaching usually to end of proximal third of second article of antennular peduncle, armed with a ventral prolongation embracing ocellary beak. Teeth on orbital hoods slender; eyes completely covered by hoods. Basal antennular article with stylocerite reaching about as far as rostrum; third article about half length of second; inner flagellum filiform, outer flagellum thickened proximally, bifurcate beyond fourth joint. Antennal scale with strong, slender lateral spine separated from and exceeding lamella distally, spine reaching about to or beyond end of antennal peduncle; basicerite well developed, angled above but lacking dorsal spine, extremity reaching to distal third of basal antennular article.

First pair of legs chelate, very unequal. Large chela with a small, acute dorsal spine at distal margin of palm; upper margin of dactyl elevated into a thick crest; carpus small, irregularly shortened; merus with dorsolateral margin convex, ending in a hooked spine. Small chela one-third length of large one; no brush of hairs on dactyl. Second pair of legs slender, weakly chelate; carpus subdivided, first joint longer than others combined. Third to fifth legs with bifurcate dactyls, both hooks nearly parallel, ventral one narrower and much shorter than dorsal.

Abdomen compressed. Telson with sides somewhat convergent; posterior angles sharp and each provided with a pair of spines, inner spine longer than outer; two pairs of strong dorsal spines, first pair at one-third, second at two-thirds length. Uropods ovate, exopod with lateral margin ending in a notch with a strong fixed spine at its outer and inner angles, between these spines a longer movable spine.

Measurements.—Length of body: ovigerous females, 13 mm.

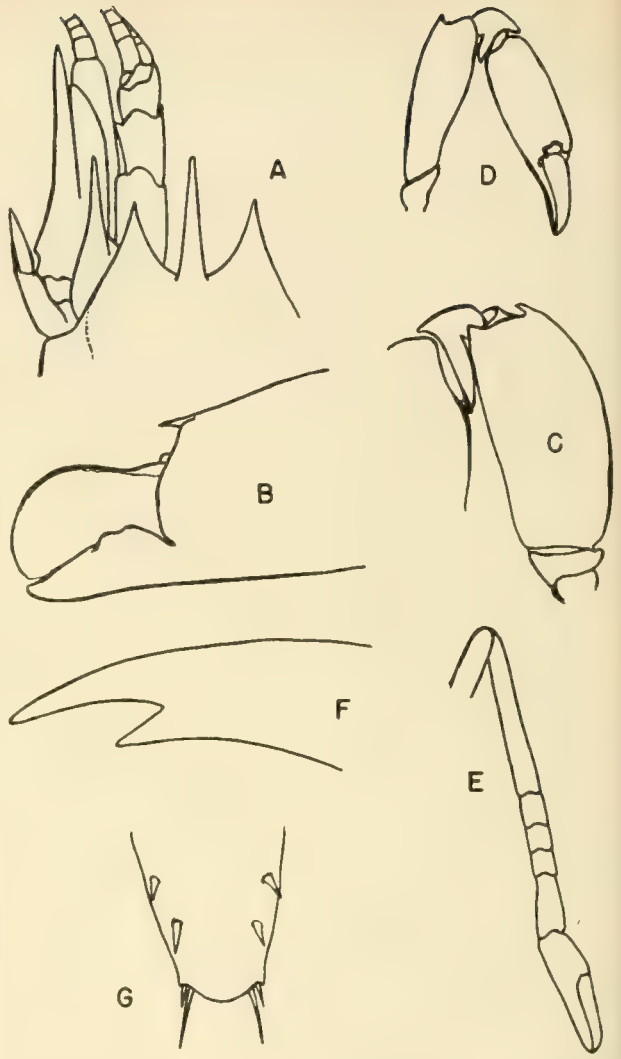

FIGURE 58.—*Synalpheus townsendi* Coutiere. A, anterior part of body in dorsal view, with appendages of left side; B, tip of large chela; C, large cheliped, merus, carpus and proximal end of propodus; D, small first cheliped; E, second leg showing subdivided carpus; F, dactyl of third leg; G, telson in dorsal view (after Coutiere, 1909).

Variations.—The rostrum is variable in length, often shorter than as described above.

Color.—Body and legs translucent pinkish red; large chela pink, changing to green on fingers.

Habitat.—Often found in large sponges; low tide mark to 56 fathoms.

Type locality.—Gulf of Mexico, *Albatross* station 2373.

Known range.—Off Beaufort, N.C., to Yucatan; through West Indies to Bahia, Brazil; Bermuda.

Remarks.—This species has been taken from offshore reefs in North Carolina at depths of 7 to 8 fathoms (Pearse and Williams, 1951), and from sponges at depths of 16 to 20 fathoms. Wass (1955) remarked that the species seems less dependent on sponges than other members of the genus taken in the Alligator Harbor area of Florida.

Ovigerous females have been taken from the Carolinas in February and August; Obregon, Mexico, in July and August; and Venezuela in September.

Synalpheus longicarpus (Herrick)

Figure 59

Alpheus saulcyi var. *longicarpus* Herrick [in part], 1892, p. 383.

Synalpheus longicarpus: Hay and Shore, 1918, p. 383, text-fig. 6; pl. 26, fig. 2 (rev.).—Verrill, 1922, p. 113, pl. 25, figs. 1a–1h; pl. 34, figs. 3, 3c; pl. 36, figs. 5, 5a (rev.).

Recognition characters.—Rostrum carinate, slender, and slightly longer than triangular, obtuse orbital hoods, reaching about to middle of basal antennular article; space between rostrum and hoods U-shaped, broadest in females. Eyes small, completely covered. Basal article of antennular peduncle with short stylocerite reaching to distal third of article; second article one-third longer than third article; inner flagellum filiform, outer branching at seventh joint, thickened proximally. Terminal article of antennal peduncle exceeding antennular peduncle; antennal scale with strong terminal spine separated from and exceeding rudimentary lamella distally; spine variable in length, often exceeding antennular peduncle by half length of distal article; lamella of scale rudimentary in males, small and variable in females; basicerite slender, acute, with an angle but no accessory spine above, tip reaching to end of second article of antennular peduncle.

First legs chelate, very unequal. Large chela elongate, somewhat ovate, about 2.75 times longer than broad; margins somewhat convex; posterior end swelled and produced backward beyond articulation with small, short carpus inserted below central axis of palm; anterior dorsal margin of palm with small, acute spine near base of dactyl; dactyl somewhat oblique at end, toothed at base, about one-fourth to one-fifth length of chela. Small chela elongate, about one-third length of larger; dactyl elongate, gently arched dorsally, a dense tuft of erect hairs on dorsal surface along most of length, cutting edge nearly straight with two apical teeth; immovable finger with three teeth, apical one stronger. Second pair of legs slender, weakly chelate; stronger in male than in female; carpus subdivided, first joint shorter than

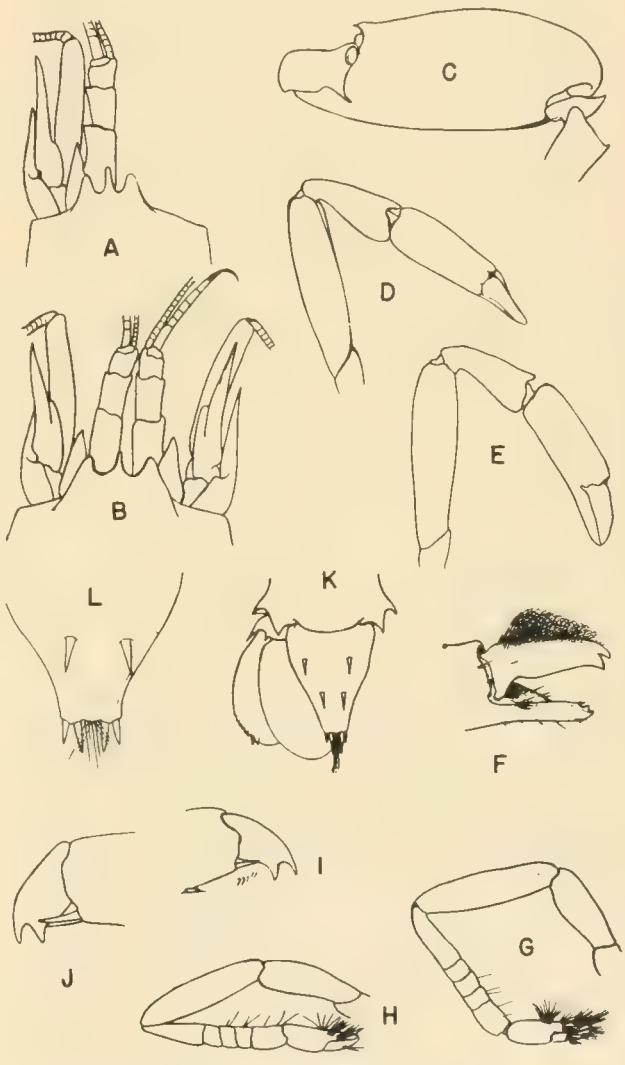

FIGURE 59.—*Synalpheus longicarpus* (Herrick). Anterior part of body in dorsal view, A, male, B, female; C, large chela; D, small first cheliped, male; E, same, female; F, fingers of small first cheliped; G, second leg of male showing subdivided carpus; H, same, female; I, dactyl of third leg; J, same in large adult; K, telson and left uropods in dorsal view, female; L, tip of telson (after Coutiere, 1909).

sum of remaining four. Third to fifth legs with dactyls bifurcate.

Sixth abdominal segment with a strong triangular tooth on each posterior angle. Telson with sinuous sides tapering to subtruncate tip; dorsal spines strong, first pair at one-third, second at two-thirds length; tip with two pairs of strong spines, inner pair slightly longer. Uropodal exopod broadly oval; lateral border spined with seven or eight denticles, a movable spine at distal end of series.

Measurements.—Length of body: ovigerous females, 16 to 22 mm.

Variations.—Length of the carpus of the small claw varies with age. The rostrum and projections on the orbital hoods may be entirely lacking or their relative lengths may vary (Wass, 1955).

Color.—Translucent white; fingers brown.

Habitat.—Lives at depths of 15 to 28 fathoms in interior of sponges; especially abundant in *Spheciospongia* (=*Spirastrella*) (Wells, Wells, and Gray, 1960). Sometimes found in sponges cast on beach during storms at Beaufort, N.C.

Type locality.—Specimens upon which Herrick's description is based were taken in the Bahamas, probably at Nassau, New Providence Island.

Known range.—Beaufort, N.C., to Yucatan, Mexico; through West Indies to Curaçao.

Remarks.—This species is common in the Carolinas and often occurs in enormous numbers in the canals of large sponges. Infestation by parasitic isopods is common, *Phryxus subcaudalis* Hay occurring on the surface of the abdomen and *Synsynella deformans* Hay in the branchial chambers.

Ovigerous females have been taken off North Carolina in August and December. The species hatches in essentially the adult form (Herrick, 1892). Coutiere (1909) and Wass (1955) remarked on the fact that few ovigerous females occur among crowded populations in sponges.

Family Ogyrididae

Caridea with first two pairs of legs chelate, nearly equal in size and not much if any larger than other legs. Carpus of second legs subdivided. Rostrum small or wanting. Eyestalks long, slender, fully exposed but with corneal surface reduced. Telson thick, obtusely pointed. Blades of uropods curved outward. Thelycum present in females (Hay and Shore, 1918).

Genus *Ogyrides* Stebbing, 1914

Stebbing, 1914, p. 31; Hemming, 1958b, p. 158.

KEY TO SPECIES IN THE CAROLINAS

a. Postrostral crest with 8 to 14 small, fixed spines ..... *limicola* (p. 74).

aa. A single movable spine behind rostrum on middorsal line ..... *alphaerostris* (p. 75).

Ogyrides limicola Williams

Figure 60

Ogyrides limicola Williams, 1955c, p. 57, fig. 1.

Recognition characters.—Rostrum short, depressed, equilaterally triangular. Postrostral carina with 8 to 14 teeth, flanked on each side by row of setae extending to tip of rostrum. Pterygostomian area broadly obtuse. Eyestalks long, lightly setiferous dorsally and dorsomedially, narrowest in middle, exceeding antennular peduncles by approximately 2.5 times corneal length. Antennal and antennular peduncles nearly equal in length; second antennular article 3 times as long as third article; stylocerite of basal article terminating in two strong acuminate spines of nearly equal length. Antennal scale and second article of antennular peduncle reaching nearly same level distally; scale evenly

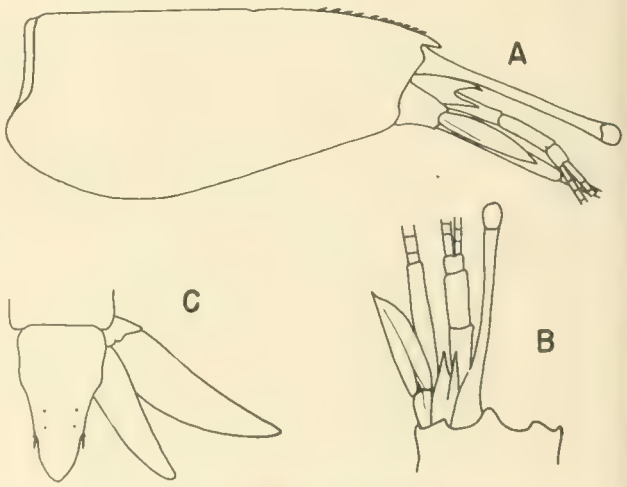

FIGURE 60.—*Ogyrides limicola* Williams. A, carapace and anterior appendages in lateral view; B, anterior appendages and portion of carapace in dorsal view; C, telson and uropods of right side in dorsal view; A–C approximately × 10 (after Williams, 1955c).

rounded medially, 3 times longer than greatest width, greatest width in basal half. Third maxilliped, when extended, exceeding eyestalks.

First legs exceeding midlength of antennal peduncle by full length of chelae; fingers of chelae pointed, agape when closed.

Telson with anterior pair of spines placed well behind lateral prominences. Uropods with exopods slightly falciform, lateral borders nearly straight. Telson with three horny ridges at proximolateral corners ventrally, and uropods with an interlocking horny eminence on basal article dorsally.

Measurements.—Length of body: ovigerous holotypic female, 16 mm.

Variations.—Individual variations are shown in the number of spines on the postrostral crest and in the lengths of the spines of the stylocerite.

Color.—Female with general body structure colorless, clear; internal organs visible; gut dark; hepatopancreas light brown; eyestalks, antennal and antennular peduncles, and distal portions of anterior appendages with red and yellow spots; uropods and sixth segment of abdomen with scattered red spots. Ovigerous females with yellow green (chartreuse) colored eggs on swimmerets (Williams, 1955c).

Habitat.—On (or in) the bottom of muddy estuaries, or in plankton; surface to 2.5 fathoms. Collections have been made in an observed bottom salinity range of 9 to 31 °/₀₀, but salinities in sounds near inlets often range higher than this.

Type locality.—Mouth of Far Creek at Engelhard, Hyde County, N.C.

Known range.—Eastern shore of Accomac County, and lower James River, Va., to Lake Pontchartrain, La.

Remarks.—The systematic confusion surrounding the two species *O. alphaerostris* and *O. limicola* was discussed by Williams (1955c). The two species are quite distinct morphologically and differ in total size, *O. limicola* being the smaller. The latter occurs most frequently in collections from estuaries. Young specimens have frequently been taken in plankton tows made at night in Bogue Sound, N.C., but adults are seldom taken by this method of collection. Occurrence of adults in samples taken with a beam trawl suggests burrowing habits similar to those described for *O. alphaerostris*, but in muddier situations and often in low salinities. The type locality and a number of other productive collecting spots in North Carolina are shallow, mud-bottomed, nontidal estuarine streams.

In North Carolina, collections of *O. limicola* have been made in all seasons of the year, and ovigerous females have been taken from May to September.

Ogyrides alphaerostris (Kingsley)

Figure 61

Ogyris alphaerostris Kingsley, 1880, p. 420, pl. 14, fig. 7.
Ogyrides alphaerostris: Stebbing, 1914, p. 31.—Hay and Shore, 1918, p. 388, fig. 11, pl. 26, fig. 9.

Recognition characters.—Rostrum depressed, equilaterally triangular, tipped with setae. A single, postrostral, movable spine. Pterygostomian area obtuse. Eyestalks long, setiferous medially, narrowest in middle, exceeding antennular peduncle by approximately twice corneal length. Antennal and antennular peduncle nearly equal in length; second article of antennular peduncle slightly over twice as long as third article;

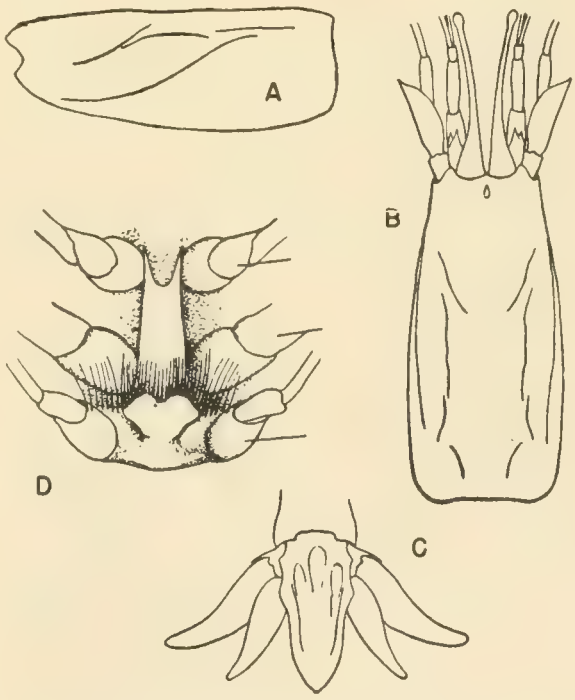

FIGURE 61.—*Ogyrides alphaerostris* (Kingsley). A carapace in lateral view; B, carapace and anterior appendages in dorsal view; C, uropods and telson in dorsal view; D, sterna of last three thoracic segments showing thelycum of female; A–C female × 5, D × 7.8 (after Hay and Shore, 1918).

stylocerite terminating in two acuminate spines; lateral spine longer. Antennal scale and second article of antennular peduncle reaching same level distally; scale evenly rounded medially, approximately three times longer than greatest width, greatest width near base. Third maxilliped, when extended, exceeding eyestalks.

First legs scarcely extending to tip of antennal scale. Second legs exceeding antennal scale by full length of chelae; fingers of chelae pointed, agape when closed.

Telson with anterior pair of spines placed approximately at level of lateral prominences. Uropods with exopods somewhat falciform, curvature greatest distally. Telson with three horny ridges at proximolateral corners ventrally, and uropods with an interlocking horny eminence on basal article dorsally.

Measurements.—Length of body: ovigerous female, 27 mm.

Color.—Body nearly transparent; red and green spots or flecks on eyestalks, antennules, and antennae; green only on distal joints of third maxillipeds; red only on basal articles of legs, on first pleopods, at bases of all pleopods, and on abdominal pleura and sterna; a conspicuous red area on sixth abdominal segment distoventrally and another around mouth.

Habitat.—Often found on firm bars of sand just offshore along open ocean in water 1 m. deep (Pearse, Humm, and Wharton, 1942); surface to 5 fathoms.

Type locality.—Eastern shore of Northampton County, Va.

Known range.—Northampton County, Va., to St. Simons Island, Ga.; Alligator Harbor, Fla., to Horn Island, Miss.

Remarks.—*Ogyrides alphaerostris* apparently is more restricted to high-salinity waters than *O. limicola*, for it has seldom been collected in the sounds of North Carolina and then only near inlets. Pearse, Humm, and Wharton (1942) described burrowing habits of the species on sandy bars and commented that members of the genus are unusual in that they have long eyestalks like *Uca*, yet are burrowers. *Ogyrides alphaerostris* burrows forward (head first), using the third maxillipeds and legs for digging and propulsion. Sand is pushed upward and over the head, the abdomen often being left above sand for a time, especially in ovigerous females. The fifth leg is held high on the sides and stroked dorsally and posteriorly, legs one to four are stroked laterally and posteriorly, and the third maxillipeds moved anteriorly and dorsally. The animals scrape food from the antennae with setose mouth parts.

Ovigerous females have been taken in July in North Carolina, and in July and August in Florida and Mississippi. The above authors imply that the breeding season is extended through the summer months.

Family **Hippolytidae**

Caridea with first two pairs of legs chelate, first pair not much stronger than rest; carpus of second pair of legs subdivided. Eyes well developed and not covered by carapace. Mandibles usually deeply cleft. Second maxillipeds with a very short dactyl.

KEY TO GENERA AND SOME SPECIES IN THE CAROLINAS

a. Carpus of second legs with three to five joints.
  b. Carpus of second legs with five joints ..... *Thor floridanus* (p. 76).
  bb. Carpus of second legs with three joints.
    c. Series of small spines (five to nine) along anterior margin of carapace below eye ..... *Latreutes* (p. 78).
    cc. Without series of small spines on anterior margin below eye.
      d. Rostrum shorter than carapace proper, with spines above and below ..... *Hippolyte* (p. 80).
      dd. Rostrum nearly twice length of carapace proper, smooth above, serrate below ..... *Tozeuma carolinense* (p. 83).
aa. Carpus of second legs with more than six joints (multiarticulate) ..... *Hippolysmata* (p. 84).

Genus ***Thor*** Kingsley, 1878

Kingsley, 1878b, p. 94.—Hemming, 1958b, p. 161.

Thor floridanus Kingsley

Figure 62

Thor floridanus Kingsley, 1878b, p. 95.—Verrill, 1922, p. 136, pl. 35, figs. 2–2f; pl. 41, fig. 1; pl. 46, figs. 2–2e; pl. 47, figs. 4, 4a.—Holthuis, 1947, p. 47, 49 (rev.).

Recognition characters.—Rostrum shorter than eyes; dorsal margin with four or five teeth, first tooth a little behind margin of orbit, distal tooth near tip making tip appear bifid; ventral margin unarmed. Carapace smooth, with prominent antennal spine below orbit. Eyes well developed. Antennules with basal article large; stylocerite long, acute, reaching beyond tip of basal article

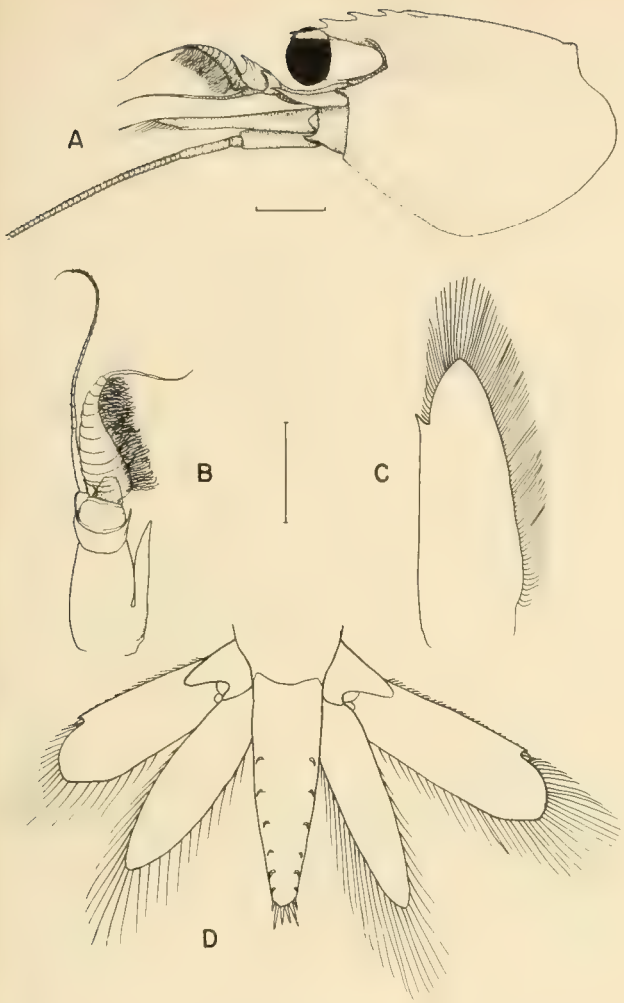

FIGURE 62.—*Thor floridanus* Kingsley. A, carapace and anterior appendages in lateral view, 1 mm. indicated; B, antennule; C, antennal scale; D, uropods and telson; B–D, 1 mm. indicated.

to level of tip of spine on second article; a tiny, erect spinule at base of stylocerite; second and third articles short; second with slender, acute spine on lateral surface; third with a thin, flat, blunt projection on upper side; inner flagellum slender, slightly longer than peduncle; outer flagellum stout basally, tapering abruptly to thin terminal portion, densely hairy on outer margin, about as long as peduncle. Antennal scale with outer margin nearly straight, terminating in a stout spine, lamella exceeding spine, an outer spine near base of scale. Third maxilliped reaching a little beyond tip of antennal scale; last article terminating in slender spines.

First legs with merus and carpus subequal; carpus with minute spinules on inner margin; chelae subcylindrical, dactyl two-fifths total length of hand. Second legs with carpus subdivided into six joints of varying lengths; chela as long as fifth and sixth carpal joints. Dactyls and propodi of third to fifth legs spinulose beneath; dactyls bifurcate but with accessory spines proximally.

Abdomen smooth; pleura of fourth, fifth, and sixth segments with posterolateral angles acute. Telson elongate, triangular, with five prominent pairs of dorsal spines a little remote from edges and spaced equidistantly in posterior three-fourths of length; tip somewhat rounded and armed with three pairs of subequal spines, outer pair shortest. Uropodal exopods with outer edge ending in a small spine flanked medially by a strong movable spine.

Measurements.—Length of body: ovigerous females, 11 to 13 mm. (Wass, 1955).

Habitat.—Among sponges, ascidians, algae, and soft corals; shallow water to 32 fathoms.

Type locality.—Key West, Fla.

Known range.—Beaufort, N.C., to Alabama; through West Indies to Curaçao and Yucatan; Bermuda.

Remarks.—This species has often been referred to *Thor paschalis* (Heller), an Indo-west Pacific form. Holthuis (1947) considered the West Indian species distinctive, and, in fact, it is the type species of the genus. As far as known, *T. floridanus* is not common in the Carolinas.

Ovigerous females have been reported (Broad, 1957c; Lunz, 1939; Verrill, 1922; Wass, 1955) or are known from collections from April to August in southeastern United States, Bermuda, and the West Indies. In addition, they are known from Cuba in November and January.

Broad (1957c) worked out the larval stages of this form, using various species of algae as food for the developing larvae. Though survival varied with species of algae fed, he considered at least certain species of algae to be an adequate diet for survival, molting, and metamorphosis. Broad described eight zoeal stages and a postlarval stage. Comparison of these stages with earlier descriptions by Lebour (1940) led Broad to question the conspecificity of *Thor* from Bermuda and the Carolinas.

Genus *Latreutes* Stimpson, 1860

Stimpson, 1860, p. 27.—Hemming, 1958b, p. 157.

KEY TO SPECIES IN THE CAROLINAS

a. Carapace and rostrum unarmed dorsally except for a single, small, median spine on gastric region; rostrum an elongate blade nearly as long as carapace *fucorum* (p. 78).

aa. Carapace strongly humped and armed dorsally with five or six spiniform teeth; rostrum a deep ovoid blade, shorter than carapace *parvulus* (p. 79).

Latreutes fucorum (Fabricius)

Figure 63

Palaemon fucorum Fabricius, 1798, p. 404.
Latreutes ensiferus: Hay and Shore, 1918, p. 390, pl. 26, fig. 13.
Latreutes fucorum: Verrill, 1922, p. 131, pl. 16, figs. 5–5b; pl. 42, figs. 2–2t; pl. 44, figs. 1–1m, 2a–2n, 3 (rev.).

Recognition characters.—Rostrum thin, nearly as long as carapace, smooth edged, broadest at base and deepest near base, slightly concave dorsally and upturned at tip, convex ventrally; tip subtruncate and armed with about five to seven small, acute spinules. Carapace smooth; a small middorsal spine on gastric region; anterior margin produced into an acute lobe below eye followed ventrally by a wide, nearly rectangular emargination and a series of four to nine small denticles at anterolateral angle; a spine removed from margin near suborbital lobe. Eyes well developed, with a tuberculate swelling anteromedially near cornea. Antennular peduncle with basal article excavate laterally; stylocerite broad, thin, cupped dorsally; distal spine on lateral border of basal article reaching about to base of third article; second and third articles short; distal border of third obscurely denticulate, outer flagellum thick at base. Antennal peduncle stout; antennal scale wide at base, tapering to acute terminal spine, scale about as long as rostrum. Third maxilliped elongated, leglike; distal article long, with eight or nine acute marginal spines.

First legs incurved, short, relatively stout, unequal; larger chela thick, proximally broad, ovate, tapering distally; dactyl wide, longer than immovable finger, with broad lateral lobe and about three denticles at tip; immovable finger bent slightly inward and arched, tip subacute or slightly bidentate; fingers hairy; carpus large, cup-shaped, broader than long; merus and carpus excavate beneath. Second legs slender; chelae slender, somewhat unequal; fingers about as long as palm, hairy at tip; carpus with three unequal joints, middle one longest. Third to fifth legs long, slender, subequal; propodi and dactyls with row of spines on lower edge.

Abdomen smooth. Telson long, narrow, tapering to narrow tip with spiniform median process flanked by two pairs of unequal spines, inner pair longer than median process; two pairs of dorsal spines, at half and three-fourths of length. Uropodal exopods with outer edge terminating in a small spine flanked medially by a movable spine.

Measurements.—Length of body: adults, 12 to 20 mm.; males smaller than females.

Variations.—The rostrum varies greatly in length, depth, and number of spines (Wass, 1955).

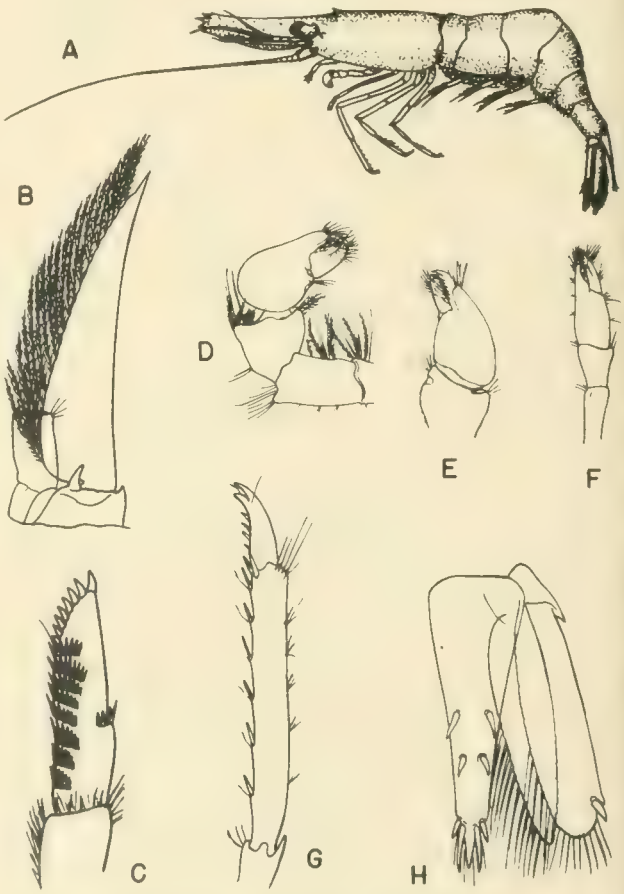

FIGURE 63. *Latreutes fucorum* (Fabricius). A, animal in lateral view, × 17 (after Bate, 1888); B, antennal scale, × 17; C, distal article of third maxilliped, × 42; D, right first cheliped, × 17; E, left first cheliped, × 25; F, second cheliped; × 17; G, distal articles of third leg, × 17; H, telson and uropods, × 17 (after Verrill, 1922).

Color.—Often nearly colorless and transparent; sometimes with body pale yellow, yellowish green, greenish brown, brown, red, black, black with white spots and bars; bright blue patches on dorsal and lateral surfaces; often mottled, striped, or barred, and corresponding in pattern to irregularly colored bits of weed (various authors).

Habitat.—Common in floating masses of *Sargassum;* surface waters.

Type locality.—Floating gulfweed.

Known range.—Newfoundland to Puerto Rico, through Gulf of Mexico to Texas; Bermuda; near the Azores and Cape Verde Islands; Cape of Good Hope (?) (Holthuis, 1951b; Sivertsen and Holthuis, 1956).

Remarks.—Ovigerous females have been observed in inshore waters of the Carolinas and adjacent western Atlantic region from July to October. They have been observed in the Gulf of Mexico from April to June. In the middle and western Atlantic they have been observed in June (Sivertsen and Holthuis, 1956). Gurney (1936a) described the first stage larva.

Pearse (1952b) reported the parasitic *Probopyrus latreuticola* (Gissler) in the gill cavity of this shrimp near Port Aransas, Texas.

Brown (1939) found four kinds of pigment in this shrimp (white, red, yellow, and blue) similar to pigments .found in *Hippolyte*, *Leander*, and *Palaemonetes* species. The red and yellow pigments respond to white background by concentration into the chromatophore centers and to black background by dispersion into the chromatophore branches. *Latreutes* has a great abundance of white pigment which may vary in color from yellowish white to clear white. Darkness produces concentration, and darkness or black background with low intensity of incident light calls forth concentration of the reflecting white chromatophores. Direct sunlight of a bright sky produces dispersion of white pigment in spite of black background. Blue patches on the animals apparently consist of blue pigment accumulated in particular white chromatophores. Brown concluded that the different color patterns in this species are not solely results of responses to particular situations, but are at least partly genetic patterns repressed or encouraged by light intensity in color of the background. The response is similar to responses in crustaceans having far less ability to change color.

Latreutes parvulus (Stimpson)

Figure 64

Rhynchocyclus parvulus Stimpson, 1866, p. 48.—1871b, p. 124.
Concordia gibberosus: Hay and Shore, 1918, p. 391, pl. 26, fig. 11.
Latreutes parvulus: Holthuis, 1947, p. 59.—1951b, p. 131, fig. 28 (rev.).

Recognition characters.—Rostrum laterally compressed, almost circular in outline in female, more elongate in male; upper margin with six to eight teeth in female, two to four in male; a few small teeth on tip; lower margin unarmed or with up to five shallow teeth; ventral part of rostrum produced somewhat backward. Carapace

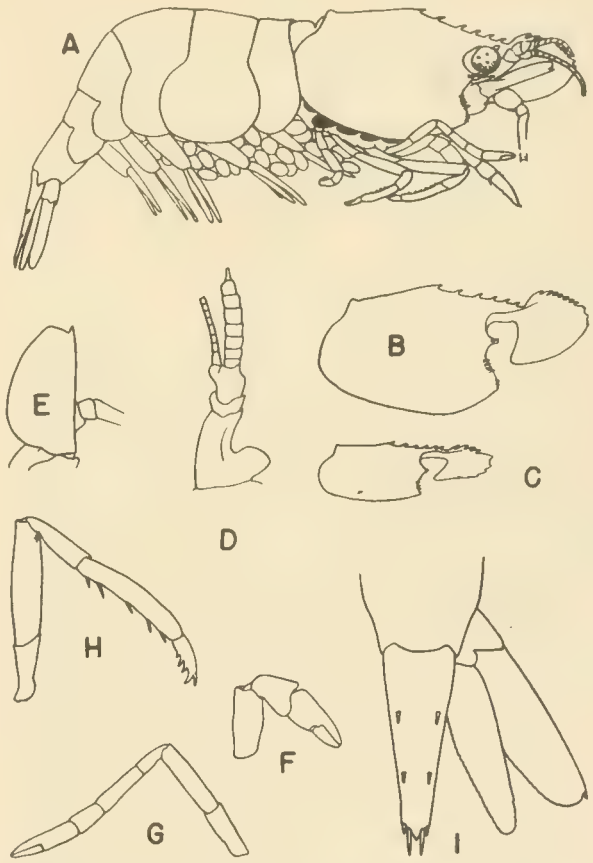

FIGURE 64.—*Latreutes parvulus* (Stimpson). A, ovigerous female in lateral view, × 6; B, carapace of ovigerous female in lateral view, × 6; C, carapace of male in lateral view, × 6; D, antennule, × 13; E, antennal scale, × 13; F, first leg, × 17; G, second leg, × 17; H, third leg, × 17; I, telson and right uropod in dorsal view, × 17 (after Holthuis, 1951b).

with middorsal row of five to seven small, erect teeth, row starting somewhat anterior to middle of carapace, extending to base of rostrum; carapace somewhat swollen in female, making an angle at base of middorsal row of teeth; upper margin nearly straight in males; anterior margin with a narrow, anteriorly directed lobe forming lower angle of orbit, a slender spine on lobe; anterolateral angle serrate with two to four teeth; between anterolateral angle and lower margin of orbit a row of three or four slender spines a bit removed from and parallel to margin. Eyes well developed; cornea globular; eyestalk with a truncated process at upper inner margin overlapping line separating cornea from stalk. Antennular peduncle with stylocerite broad and rounded, hollowed above and together with basal article of penduncle forming concavity for reception of eye; second article of peduncle much shorter than third; upper flagellum shorter than lower, with seven or eight broad and one or two narrow joints. Antennal scale about twice as long as broad, overreaching antennular and antennal peduncles, but not reaching end of rostrum; outer margin nearly straight, ending in a small tooth reaching about as far as lamella; a small spine on outer surface of peduncle near base of scale.

First legs equal, short, thickset, slightly overreaching base of antennal scale; fingers somewhat shorter and narrower than palm, tips of fingers ending in dark-colored nails; palm broadened posteriorly; carpus somewhat conical, about as long as palm. Second legs more slender, reaching about to end of antennal peduncle; chelae with fingers shorter than palm; carpus almost twice length of chela, three-jointed, median joint longest; merus two-thirds as long as carpus. Third to fifth legs with dactyls ending in a sharp tooth, posterior margin with four comblike teeth progressively smaller proximally.

Abdomen smooth. Telson triangular; with two pairs of dorsal spines at half and three-fourths length; tapering to a narrow tip with spiniform median process flanked by two pairs of spines, inner pair longest; terminal portion with feathered setae. Uropodal exopods with outer margin ending in a small spine flanked medially by a movable spine.

Measurements.—Length of body: 7 to 12 mm.; males smaller than females.

Variations.—Shape of the rostrum, as well as its spination, is subject to some variation.

Habitat.—Littoral waters from (in?) sponges, and among shells and hydroids; surface to 24 fathoms.

Type locality.—St. Joseph Island, Tex.

Known range.—Beaufort, N.C., to Texas; Cuba; Puerto Rico; French Guiana; Rio de Janeiro, Brazil; Sierra Leone, West Africa.

Remarks.—For many years this species has been known as *Concordia gibberosus* Kingsley or *Latreutes gibberosus* (Kingsley). Holthuis (1947) showed that these names fall into the synonymy of Stimpson's species.

Latreutes parvulus is not known to be common anywhere in its range. It has been taken throughout the year in the Carolinas. Ovigerous females have been taken throughout the year in various parts of the range north of the equator and in February in Brazil.

Genus ***Hippolyte*** [Leach, 1814]

Verrill, 1922, p. 124.—Holthuis, 1947, p. 53.—Hemming, 1958b, p. 157.

KEY TO SPECIES IN THE CAROLINAS

a. Basal article of antennular peduncles without distal spines dorsally ..... *pleuracantha* (p. 80).
aa. Basal article of antennular peduncles with distal spines dorsally ..... *zostericola* (p. 82).

Hippolyte pleuracantha (Stimpson)

Figure 65

Virbius pleuracanthus Stimpson, 1871b, p. 127.
Hippolyte pleuracantha: Hay and Shore, 1918, p. 390, pl. 26, fig. 8.—Holthuis, 1947, p. 15 (rev.).

Recognition characters.—Body smooth, with tufts of plumose hairs on dorsal surface of carapace and abdomen, tips of abdominal pleura, and distal portion of eyestalks. Rostrum rather stout at base, thin distally, slightly decurved, armed dorsally with one to three teeth and ventrally with one to three teeth near tip; tip reaching about to end of antennular peduncle; a strong spine on each side at base of rostrum. Anterior margin of carapace produced into a lobe below eye followed ventrally by an antennal spine, an emargination at base of antenna followed by a slightly produced, broadly rounded anterolateral angle; hepatic spine strong. Eyes well developed. Antennular peduncle with basal article long and broad, stylocerite slender, lanceolate, reaching

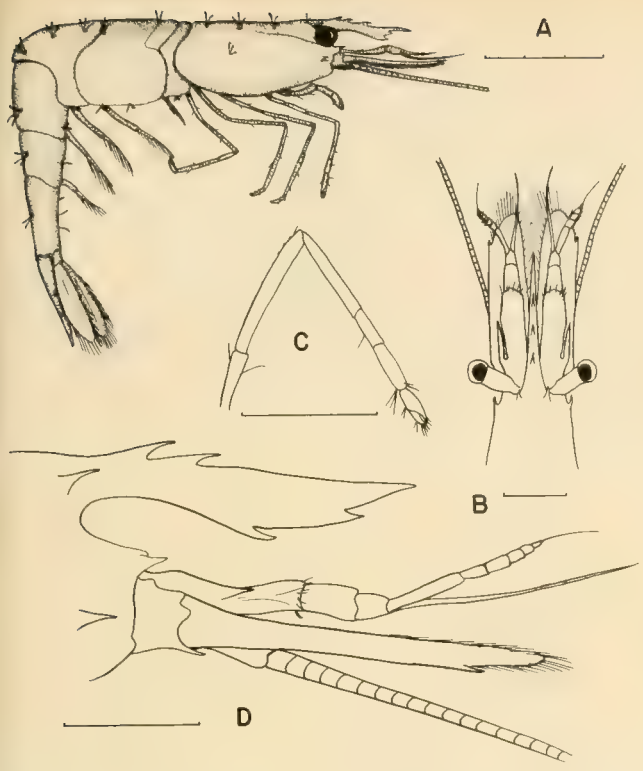

FIGURE 65.—*Hippolyte pleuracantha* (Stimpson). A, animal in lateral view, 3 mm. indicated; B, anterior portion of body in dorsal view; C, second leg; D, anterior portion of body in lateral view; B–D, 1 mm. indicated.

about to middle of article and separated from lateral border of article by about width of stylocerite, article ending in a short, broad, elevated, bladelike projection, a short spine at anterolateral corner under blade; second and third articles much shorter than first; antennular flagella of about equal length; outer ramus stout, broadest in middle, tapering to slender distal portion, hairy on ventral border. Antennal scale large, exceeding rostrum and reaching nearly to end of antennular flagella, length a little over three times width; outer margin slightly concave, terminating in a small spine, spine exceeded by lamella; a spine near base of scale.

First legs short, nearly equal, reaching a little beyond base of distal article of antennal peduncle; chelae setose, palm inflated, fingers about half length of palm, cutting edges finely serrate; carpus irregularly conical in shape, about three-fourths length of chela, lower outer border with spiniform setae. Second legs slender, reaching to tip of antennular peduncle; carpus longer than merus, divided into three joints; fingers two-fifths length of chelae, tips of cutting edges with spines; chelae hairy. Third to fifth legs long; third reaching to tip of antennal scale; dactyls with series of spines in comblike arrangement on inner border; propodi spined on inner border.

Abdomen strongly bent at third segment; posterior portion of third segment raised with hoodlike projection overhanging fourth segment. Telson with two pairs of dorsal spines on lateral border, one about at half, another at three-fourths length; tip truncate, bearing three pairs of spines, inner two pairs nearly equal, outer pair much shorter. Uropodal exopods with lateral border ending in a small spine flanked medially by a movable spine.

Measurements.—Length of body: ovigerous females, 12 to 18 mm.; males somewhat smaller.

Variations.—The rostrum in this species varies conspicuously in number of teeth, in shape from lateral view, and in length. Dorsal and ventral rostral teeth occur in all combinations from 1/1 to 3/3. Males are more slender than females.

Color.—Usually mottled brown or red, often a bright green.

Habitat.—Extremely abundant in beds of vegetation (*Zostera* and *Diplanthera*) in sounds and bays. Also found among rocks of jetties.

Type locality.—Norfolk Harbor, Va., and Somers Point, Great Egg Harbor, N.J.

Known range. New Jersey to Galveston, Tex.; Bermuda.

Remarks.—The two species, *Hippolyte pleuracantha* and *H. zostericola*, have been much confused over the years, and it is not at all certain that differences pointed out here adequately distinguish them. No attempt has been made here to give complete synonymies. This task must be approached by a thorough revisionary work in which all existing collections are studied.

In general, it can be stated that *H. pleuracantha* has no prominent distal spines on the basal article of the antennular peduncle; it has a relatively shorter rostrum, and appears to be somewhat larger than *H. zostericola*. *Hippolyte zostericola* has a prominent, distal, dorsal pair of spines on the basal article of the antennular peduncle. I am much indebted to L. B. Holthuis for pointing out

the latter character to fellow workers on the American coast.

Because identifications in the literature are probably confused, the geographic limits of the species given here must be regarded with reserve.

Ovigerous females of *H. pleuracantha* occur in North Carolina at least from April to October in the Beaufort area. Gurney (1936b) pointed out some differences between adults of *H. pleuracantha* and *H. zostericola* (as well as other species of *Hippolyte*) and described four larval and two postlarval stages of what he considered to be a Bermudian subspecies, *H. pleuracantha bermudensis*.

Hippolyte zostericola (Smith)

Figure 66

Virbius zostericola Smith, 1873c, p. 550, pl. 3, fig. 11.
Hippolyte zostericola: Holthuis, 1947, p. 16.

Recognition characters.—Body smooth. Rostrum rather stout at base, thin distally, slightly decurved, armed dorsally with three or four teeth and ventrally with two to five teeth distally; tip reaching beyond antennular peduncle and often nearly to tip of antennal scale; a strong spine on each side at base of rostrum. Anterior margin of carapace produced into a prominent narrow lobe below eye followed ventrally by an antennal spine; a shallow emargination at base of antenna and a broadly rounded anterolateral angle; hepatic spine well developed. Antennular peduncle with basal article long and broad, stylocerite slender, divergent at tip and well separated from article, basal article terminating in a pair of well-developed spines on anterolateral corner; second and third articles much shorter than first; antennular flagella of about equal length, outer ramus stout basally, tapering to slender distal portion, hairy on ventral border. Antennal scale large, slightly exceeding rostrum and reaching nearly to end of antennular flagella, length a little over three times width; outer margin slightly concave, terminating in a small spine, spine exceeded by lamella; a spine near base of scale.

First legs short, nearly equal, reaching base of distal article of antennal peduncle; chelae lightly setose, palm inflated, fingers about half length of palm, cutting edges finely serrate;

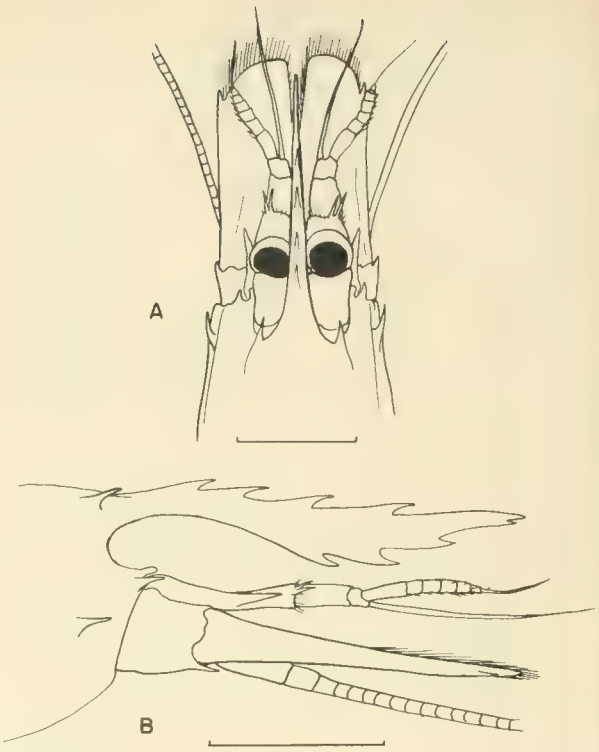

FIGURE 66.—*Hippolyte zostericola* (Smith). A, anterior portion of body in dorsal view; B, anterior portion of body in lateral view; 1 mm. indicated.

carpus irregularly conical in shape, about three-fourths length of chela, lower outer border with spiniform setae. Second legs slender, reaching to distal end of basal article of antennular peduncle; carpus longer than merus, divided into three joints; fingers about two-fifths length of chelae, tips of cutting edges with spines; chelae hairy. Third to fifth legs long; third reaching to tip of antennal scale; dactyls with series of spines in comblike arrangement on inner border; propodi spined on inner border.

Abdomen strongly bent at third segment; posterior portion of third segment raised with hoodlike projection overhanging fourth segment. Telson with two pairs of dorsal spines on lateral border, one at half, another at three-fourths length; tip truncate, bearing three pairs of spines, inner two pairs about equal, outer pair much shorter. Uropodal exopods with lateral border ending in a small spine flanked medially by a movable spine.

Measurements.—Length of body: ovigerous females, 10 to 12 mm.; males somewhat smaller.

Variations.—The rostrum in this species varies considerably in number of teeth, shape from lateral view, and relative length. Dorsal and ventral teeth have been observed in the combinations 3/3, 3/4, 3/5, 4/2, 4/4, and the range of variation may be greater than this because only a few specimens from the Beaufort, N.C., area have been studied. Males are more slender than females.

Color.—Bright green, pale or translucent tinged with green; sometimes specked with reddish brown and with a broad median band of dark brown extending whole length of body (Smith, 1873c).

Habitat.—Beds of vegetation such as eelgrass.

Type locality.—Vineyard Sound, Mass.

Known range.—Southern Massachusetts, through Gulf of Mexico and West Indies to Curaçao (Holthuis, 1947).

Remarks.—Differences between this species and *H. pleuracantha* are discussed in the account for *H. pleuracantha.* Ovigerous females have been found in North Carolina in September.

Genus ***Tozeuma*** Stimpson, 1860

Stimpson, 1860, p. 26.—Holthuis, 1955, p. 112 (rev.).

Tozeuma carolinense Kingley. Arrow shrimp

Figure 67

Tozeuma carolinensis Kingsley, 1878b, p. 90.—1880, p. 413.—Schmitt, 1935a, p. 155.
Tozeuma carolinense: Rathbun, 1901, p. 114.—Hay and Shore, 1918, p. 391, pl. 27, fig. 2.
Angasia carolinensis: Holthuis, 1947, pp. 17, 61.

Recognition characters.—Body elongate, compressed. Rostrum slender, almost twice as long as remainder of carapace, inclined slightly upward distally, rounded and unarmed dorsally, base somewhat flattened and horizontal, deepest anterior to orbit and decreasingly lamellate distally; ventral border with many appressed teeth. Carapace smooth, polished; a strong spine at either side of base of rostrum; anterior margin produced into a triangular tooth below eye; anterolateral angle with a spine. Eyes well developed. Antennular peduncle rather slender; first article longest, with slender stylocerite slightly exceeding distal border; second and third articles progressively shorter; outer flagellum thick and much shorter than inner, neither quite reaching tip of antennal scale. Antennae longer than rostrum; antennal scale lanceolate, less than half length of rostrum; basal antennal article with a strong ventrolateral spine on anterior border.

Legs relatively short; first pair very short, stout, hand inflated, fingers curved, closing completely, spines on fingers dark colored; second pair slender, longer, carpus with three joints, proximal joint nearly as long as merus; legs three to five with comblike spines on curved dactyls.

Abdomen smooth; strongly bent between third and fourth segments; third segment of male bearing a low dorsal hump; fifth segment with a spine at each side of posterior border; sixth with a spine at posterolateral angle and a broad spine at base of telson. Elements of tail fan long and narrow. Telson with one pair of dorsal spines at midlength, another at three-fourths length; tip with a strong pair of median spines flanked by a weak lateral pair. Uropodal exopods with outer border terminating in a small spine flanked medially by a movable spine.

Measurements.—Length of body: ovigerous females, 28 to 50 mm.

Variations.—The humped third abdominal segment is pronounced in young individuals of both sexes.

Color.—Apparently varying to some degree depending on background; shades of green from light yellowish green to rich deep green, or occasionally brownish or red in beds of *Diplanthera wrightii* and *Zostera marina* (Bryce, 1961); purple on alcyonarian corals *Antillogorgia* and *Pterogorgia* (Voss, 1956); nearly colorless (Verrill, 1922).

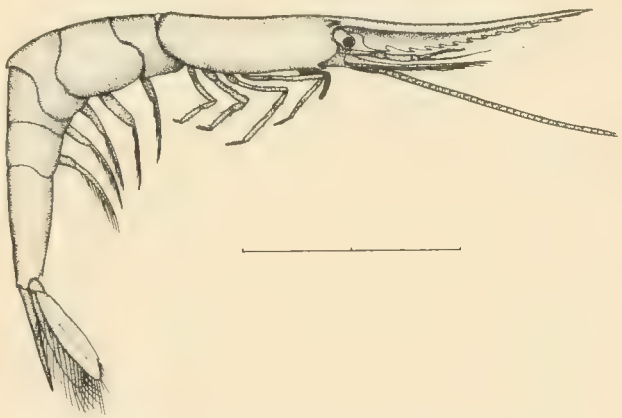

FIGURE 67.—*Tozeuma carolinense* Kingsley. Female in lateral view, 10 mm. indicated.

Habitat.—Common in beds of vegetation or similar habitats in shallow water, this species often swims in a vertical position and rests in a clinging position on blades of grass. It blends well with the background because of shape and color and is aptly named "arrow shrimp". Surface to 41 fathoms (Holthuis, 1947).

Type locality.—Fort Macon, N.C.

Known range.—Vineyard Sound, Mass., to Colon, Panama; through West Indies to Curaçao.

Remarks.—Bryce (1961) gave general ecological observations on *T. carolinense* along with a detailed study of larval development. The adults apparently feed by grazing on faunal and floral growths on marine grasses.

In North Carolina, ovigerous females are present from May to October, with one doubtful record in February. Elsewhere they have been taken in February from Bimini, March to November in Florida and Louisiana, and in December from Puerto Rico.

Bryce found that larvae hatched from ovigerous females and reared in culture dishes usually passed through eight or nine larval stages before metamorphosing into postlarvae. However, the larvae did not always transform at these stages, and, in one group reared in early fall, continued molting for an indefinite number of stages. One individual passed through 25 larval stages before the experiment was terminated. Variations in larval stages and examples of asymmetry were discussed, as were the effects of diet and temperature.

Genus ***Hippolysmata*** Stimpson, 1860

Stimpson, 1860, p. 26.—Holthuis, 1955, p. 115.—Hemming, 1958b, p. 156.

KEY TO SPECIES IN THE CAROLINAS

a. Rostrum not exceeding antennular peduncles *wurdemanni* (p. 84).

aa. Rostrum greatly exceeding antennular peduncles *oplophoroides* (p. 85).

Hippolysmata (Hippolysmata) wurdemanni (Gibbes)

Figure 68

Hippolyte wurdemanni Gibbes, 1850, p. 197.

Hippolysmata wurdemanni: Hay and Shore, 1918, p. 392, pl. 26, fig. 12.

Recognition characters.—Rostrum reaching distal end of second article of antennular peduncle, slightly decurved, armed dorsally with four or five teeth and ventrally with three to five teeth Carapace smooth; carinate dorsally on anterior half with a spine near base of rostrum about midway between rostral tip and posterior border; anterior margin with a strong antennal spine; anterolateral corner rounded. Eyes well developed. Basal article of antennular peduncle large, stylocerite slender, flattened, pointed, reaching a little beyond middle of article; second and third articles progressively shorter; inner flagellum slender; outer flagellum with about 20 to 30 thickened basal joints. Antennal scale long, narrow; outer margin about straight, terminating in a strong spine; lamella of scale truncate distally, about equal to spine.

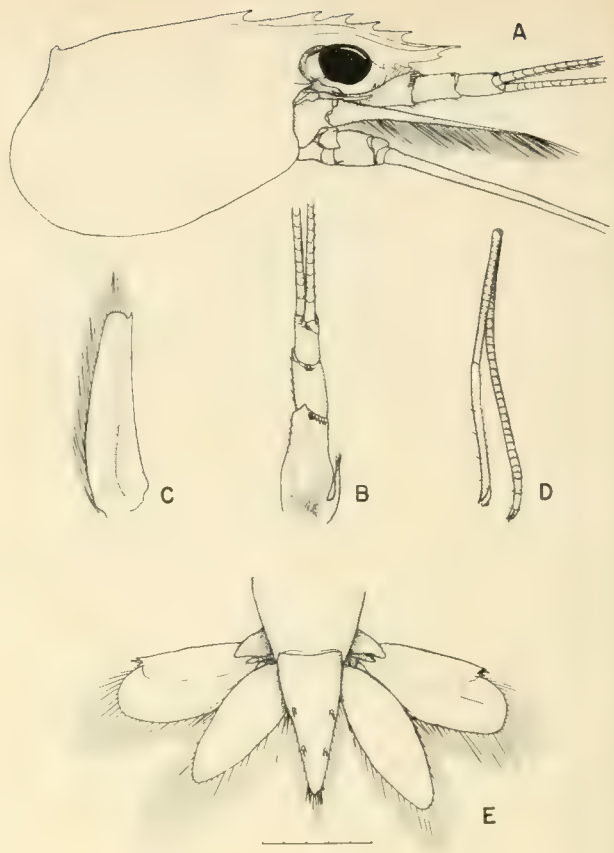

FIGURE 68.—*Hippolysmata (Hippolysmata) wurdemanni* (Gibbes). A, anterior portion of body in lateral view; B, antennule; C, antennal scale; D, second leg; E, uropods and telson in dorsal view; A–E, 5 mm. indicated.

Epipods on first four pairs of legs. First legs stout, about equal, reaching to end of antennal

scale; fingers about one-third length of palm, spines at tips of fingers darkened; carpus and hand of nearly equal length. Second legs much longer, slender; chela small; carpus divided into about 30 joints, last joint longest. Third to fifth legs not so slender as second; dactyls with a few coarse spines on inner border.

Abdomen smooth; posterolateral angle of fifth and sixth segments acute. Telson tapering to nearly truncate tip with a minute median projection flanked by two long, slender spines and outside these a short spine on each side; armed dorsally with two pairs of dorsal spines, anterior pair at one-third length, posterior pair at two-thirds length. Uropodal exopods with outer margin ending in two distinct teeth, between these a slender movable spine.

Measurements.—Length of body: males, 28 to 54 mm.; ovigerous females, 38 to 55 mm. (Wass, 1955, in part).

Variations.—Individuals from the northern extreme of the range differ in some respects from those in South America (Holthuis, 1959). The rostrum in South American specimens has four to seven dorsal teeth, and in specimens from the United States, four or five. Some southern specimens have stylocerites nearly as long as the basal antennular articles. In southern specimens, the tip of the lamella on the antennal scale is more truncate than in northern specimens. The second leg in Guiana material is more slender than in northern material, and the number of articulations in the carpus is higher, 33–37 as opposed to 27–31.

Color.—Translucent white with beautiful longitudinal and transverse markings of red.

Habitat.—Commonly found on stone jetties or among hydroids growing on piles or buoys; surface to 16 fathoms.

Type locality.—Key West, Fla.

Known range.—Lower Chesapeake Bay to Port Aransas, Tex.; Surinam; French Guiana; Mamanguape, São Paulo, Brazil.

Remarks.—Ovigerous females have been reported in January from Florida and in May from the Guianas (Holthuis, 1959; Wass, 1955). They have been collected in April and August from North Carolina, and in August from Louisiana.

Subgenus *Exhippolysmata* Stebbing, 1915

Stebbing, 1915, p. 94.

Hippolysmata (Exhippolysmata) oplophoroides Holthuis

Figure 69

Hippolysmata (Exhippolysmata) oplophoroides Holthuis, 1948, p. 1106.—1959, p. 112, fig. 17.

Recognition characters.—Rostrum long, slender, directed somewhat upward, reaching beyond antennal scale by nearly half of length; basal portion elevated into a crest bearing 9 to 10 closely placed teeth, one tooth some distance behind crest, remainder of upper margin with 1 to 6 widely separated teeth; ventral margin with 10 to 14 teeth. Carapace coarsely pitted; anterior margin produced into a slight lobe below eye closely followed ventrally by an antennal spine; a pterygostomian spine at anterolateral angle. Eyes well developed. Basal article of antennular peduncle with stylocerite rather broad and pointed, reaching beyond middle of article; second article somewhat longer than third; upper flagellum simple with about 20 to 25 basal joints thickened, hairy below. Antennal scale almost

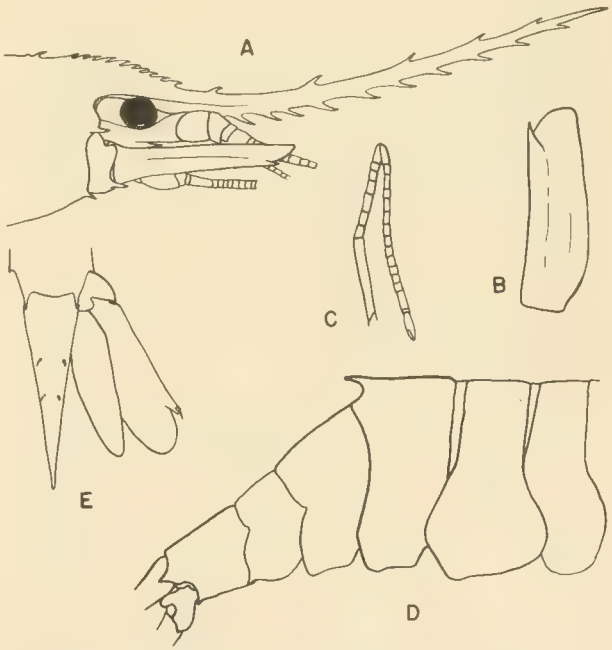

FIGURE 69.—*Hippolysmata (Exhippolysmata) oplophoroides* Holthuis. A, anterior portion of body in lateral view, × 3.5; B, antennal scale, × 4; C, second leg, × 4; D, abdomen in lateral view, × 3.5; E, telson and right uropod in dorsal view, × 3.5 (after Holthuis, 1948).

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three times as long as broad; outer margin slightly concave, ending in a strong tooth; lamella of scale exceeding spine; outer spine near base of scale directed ventrally.

Epipods on first four pairs of legs small but distinct. First legs equal, reaching somewhat beyond end of antennal peduncle; fingers short and blunt, immovable finger ending in a dark colored, sharp point fitting between two dark points on end of dactyl, outer surface of fingers convex, inner surface concave, fingers about five-eighths length of palm; carpus slightly shorter than chela and three-fourths length of merus. Second legs slender; slightly unequal in size, reaching almost to end of third maxilliped; chela small and slender; carpus five times length of chela and divided into 13 to 15 joints, first and last joints longest. Third to fifth legs slender; dactyls simple.

Abdomen coarsely and shallowly pitted; third segment with a dorsal carina ending in a strong, posteriorly directed spine; pleura of second to fourth segments produced posteroventrally in a narrowly rounded tip, pleura of fifth and sixth ending in a distinct sharp tooth; posterolateral angle of sixth spiniform. Telson tapering gradually to a slender point; dorsal surface with two pairs of spines, anterior pair at one-third length, second pair closer to first pair than to tip. Uropods elongate; outer margin of exopod ending in two distinct teeth, between these a slender movable spine.

Measurements.—Length of body: ovigerous females, 47 to 79 mm.

Variations.—In the case of a rostrum with one distal tooth dorsally, there were suggestions of three other small, malformed teeth.

Color.—General color pink; rostrum and anterior part of carapace pink, posterior part of carapace white and yellowish; abdomen white with pink most pronounced along posterior margins of first to fourth segments, spine on third segment almost red, fifth and sixth segments entirely pink; tail fan red, pink at base; antennular and antennal flagella pink; legs red, sometimes purplish distally; pleopods red; eggs yellow or greenish (Holthuis, 1959).

Habitat.—The species has been taken near shore, often in estuaries (15.89 °/₀₀ over mud bottom) (Holthuis, 1959); 4 to 15 fathoms.

Type locality.—Mouth of Suriname River near Resolutie, Surinam.

Known range.—Off Cape Fear River, N.C., to Port Aransas, Tex.; British Guiana to Santos Harbor, São Paulo, Brazil.

Remarks.—Most information on this recently described species is summarized in Holthuis' (1959) account. Ovigerous females have been reported from December to July in South America and from August to October in the Carolinas. The species is more abundant than *Xiphopeneus* in British Guiana but apparently less abundant to the eastward in the other Guianas. Records from the United States are sporadic.

Family **Processidae**

Rostrum horizontal with dorsal surface of carapace. First pair of legs asymmetrically chelate; first leg of one side ending in a simple clawlike dactyl. Second pair of legs minutely chelate; slender; with segmented carpus.

Genus ***Processa*** Leach, [1815]

Holthuis, 1955, p. 116 (rev.).—Hemming, 1958b, p. 143.

Processa bermudensis (Rankin)

Figure 70

Nika bermudensis Rankin, 1900, p. 536.

Processa canaliculata: Verrill, 1922, p. 138.—Schmitt, 1935a, p. 169 (part).

Processa bermudensis: Gurney, 1936c, p. 624, figs. 44–52 (rev.).—Lebour, 1941, p. 410, figs. 28–33.—Holthuis, 1959, p. 120.

Recognition characters.—Rostrum slender, nearly straight, extending about two-thirds length of eye, bifid at end with upper process shorter than lower, a few hairs between tips. Carapace lacking antennal spine; anterior border rounded, somewhat sinuous. Eyes large, shorter than basal antennular article. Antennular peduncle with basal article excavate dorsally, longer than succeeding two articles combined, stylocerite short, somewhat truncate; second article about half again as long as third; inner flagellum filiform; outer flagellum thick, fusiform at base, slender distally, hairy, about as long as peduncle. Antennal scale about six times as long as wide; sides nearly parallel, truncate terminally; lateral spine small, slightly exceeding lamella; antenna a little longer than body. Third maxilliped with ter-

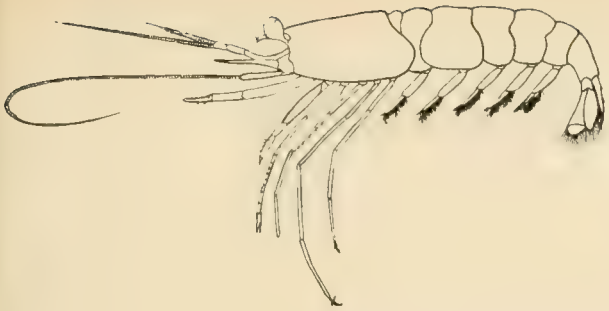

FIGURE 70.—*Processa bermudensis* (Rankin). Animal in lateral view (after Rankin, 1900).

minal article and a portion of adjacent article extending beyond antennular peduncle.

First pair of legs strong; chelate on right side; carpus a little over one-third length of merus, length about 1.5 times width; palm 1.5 times length of dactyl; left leg not chelate, carpus three times as long as wide and about two-thirds length of propodus. Second legs long, slender, unequal, chelate; carpus and merus subdivided; right leg with 18 carpal, 12 meral joints; left leg with 17 carpal, 6 meral joints; merocarpal bend of right leg reaching to or beyond end of antennal scale. Remaining legs long, slender; third shortest; fourth slightly longer than fifth; dactyls simple; propodus of fifth leg with groups of long setae, a single small spine at end and one to five additional spines along article.

Abdomen with pleura rounded. Telson three times as long as basal width; two pairs of large dorsolateral spines, first pair close to anterior end; tip subacute, armed with two pairs of stout spines, and a strong median pair of feathered setae, outer spines short, intermediate spines long. Uropods elongate; outer border of exopod ending in an acute spine flanked medially by a strong movable spine.

Measurements.—Length of body: males 14 to 16 mm.; females, 50 mm.

Variations.—The first pair of legs is usually chelate on only the right side but this asymmetry may be reversed. Relative length of the carpus of the first legs changes with age.

Color.—Larvae pale brown with glistening white chromatophores; whole body pale (Lebour, 1941).

Habitat.—Oceanic water; surface to possibly 180 fathoms.

Type locality.—Harrington Sound, Bermuda.

Known range.—Bermuda; North Carolina (restricted to recently identified material).

Remarks.—Gurney (1936c), Lebour (1941), and Holthuis (1959) have all pointed out the confusion which exists concerning identity of the species of *Processa* in the Western Atlantic. Formerly, the species found in the Western Atlantic were lumped under the name *P. canaliculata*, a name now restricted to a species in European waters (Lebour, 1936), but Lebour (1941) showed that three or perhaps four species occur at Bermuda. It is likely that more than one species occurs in the Carolinas as well.

From descriptions given by the above authors, it appears that one species occurring in the Carolinas is *P. bermudensis*, a species lacking antennal spines, although the stylocerite in North Carolina material is not shaped exactly as that shown in Gurney's illustrations. In addition, there is apparently a second species (represented by a few immature specimens in the Institute of Fisheries Research collection, all taken in night plankton tows in Bogue Sound) which has an antennal spine present, shorter legs than *P. bermudensis*, fewer joints in the carpi of the second legs than the above, and exhibits considerable variation in spination of the third and fourth legs. These specimens appear to be close to Lebour's *P. wheeleri*, but because they are so few in number and immature it is best to reserve determination until more material is available for study.

Lebour (1941) showed that *P. bermudensis* larvae are common in the plankton almost throughout the year in Bermuda, and adults were commonly found in the dredge at night, with ovigerous females occurring at least from June to October. Gurney (1936c) described eight larval stages.

Pearse (1934) too *P. "canaliculata"* from loggerhead sponges at Tortugas, Florida.

Family **Pandalidae**

Rostrum long and slender, laterally compressed, armed with teeth or spines. Eyes well developed. Mandibles with incisor process and a two or three-jointed palp. First pair of legs simple or microscopically chelate; second pair long, slender, chelate, carpus subdivided.

Genus *Pantomus* Milne Edwards, 1883

Rathbun, 1901, p. 117.—Hemming, 1958b, p. 159.

Pantomus parvulus Milne Edwards

Figure 71

Pantomus parvulus Milne Edwards, 1883, pl. 26, fig. 1, 1a.—Rathbun, 1901, p. 118.—Schmitt, 1935a, p. 138.

Recognition characters.—Rostrum longer than carapace, articulated with anterior margin of carapace; basal portion with three dorsal spines; lower margin with numerous slender overlapping spines; terminal half directed upward; tip bifid, lower prong longest. Carapace carinated on anterior half and armed with three spines, posterior two near together and movable, anterior spine adjoining articulation of rostrum; antennal and pterygostomian spines present. Eyes large. Antennular peduncle with basal article excavate above and longer than nearly equal second and third articles combined; stylocerite wide, broadly pointed, inner margin sinuous, tip reaching to midlength of cornea; upper flagellum about twice diameter of lower flagellum at base. Antennal scale, slender, reaching two-thirds length of rostrum, broadest near base; lateral spine exceeded by lamella.

Third maxilliped and first pair of legs reaching to tip of antennal scale. Second pair of legs longer than first; carpus subdivided; one leg with 15 to 17 carpal joints, other leg shorter, with 10 to 12 carpal joints. Third to fifth legs progressively longer than second pair.

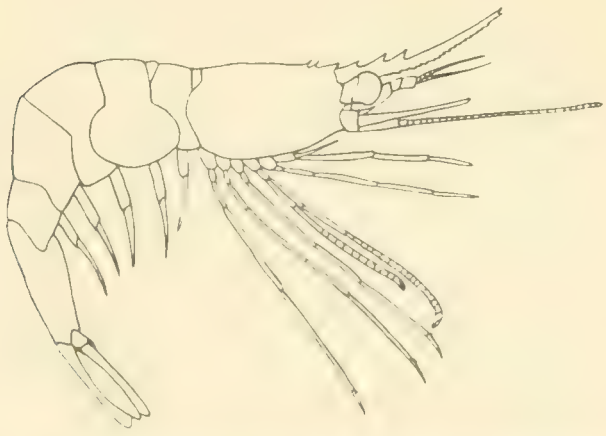

FIGURE 71.—*Pantomus parvulus* Milne Edwards. Animal in lateral view (after Milne Edwards, 1883).

Abdomen with third segment broadly carinated on posterior half; sixth segment elongate, 2.5 times length of fifth. Telson nearly as long as sixth segment, slender; sides concave, tapering to tip ending in a small, median, bulblike enlargement; two pairs of spines at tip, outer pair longest and sinuous at base, inner spines shorter, arising on terminal bulb; a row of seven or eight small dorsolateral spines on each side in distal two-thirds of length. Uropods long, narrow; exopod with lateral border ending in a slender movable spine.

Measurements.—Length of body: ovigerous female, approximately 30 mm.

Variations.—Among four of the cotypes, the rostrum varies somewhat in length and the number of carpal segments in the second legs is subject to variation.

Habitat.—Seventy-five to 248 fathoms.

Type locality.—Northern part of Yucatan Bank, lat. 23°13′ N. long. 89°16′ W., 84 fathoms.

Known range.—Cape Lookout, N.C., to Yucatan, Mexico; Puerto Rico; St. Croix, V.I.

Remarks.—The Catalogue of the Books, Manuscripts, Maps and Drawings in the British Museum (Natural History), vol. VI, Supplement, 1922, lists Milne Edwards' 1883 paper as follows: "The title-page (wanting to this copy), the 'Liste des Planches,' and many of the plates themselves are lithographed. Only fifty copies were issued and sent mostly to fellow workers, but a few were sold, (See letter by the Author in 'Ann. and Mag. Nat. Hist.' Vol. vi, 1890, p. 471)."

Family **Crangonidae**

First pair of legs subchelate, stouter than second. Second pair of legs slender, equal; carpus not subdivided; minutely chelate or simple. Rostrum small, usually dorsally flattened, not toothed.

Genus *Crangon* Fabricius, 1798

Holthuis, 1955, p. 134.—Hemming, 1958b, p. 108.

The name *Crangon* confused with the name *Alpheus* during the first half of this century, had doubtful status until nomenclatural stability was effected by the International Commission on Zoological Nomenclature (Opinion 334). The Official List of Generic Names in Zoology (Hemming,

1958b) now lists *Crangon* Fabricius, 1798, as the correct generic name for the species here considered, and the Official Index of Rejected and Invalid Generic Names in Zoology (Hemming, 1958a) lists the suppressed generic name *Crangon* Weber, 1795, and the invalid name *Crago* Lamarck, 1801, formerly applied to the species here considered.

Crangon septemspinosa Say

Figure 72

Crangon septemspinosa Say, 1818, p. 246.
Crago septemspinosa: Hay and Shore, 1918, p. 396, pl. 27, fig. 9.—Rathbun, 1929, p. 20.

Recognition characters.—Rostrum shorter than eyestalks, unarmed, tip obtuse. Carapace somewhat depressed, subcylindrical; dorsal surface with a small appressed spine back of rostrum; anterior margin with suborbital spine obtuse; antennal spine strongly produced, equaling or slightly exceeding eyes and with a minute spine below; hepatic spine well developed; anterior portion of carapace with two impressed lines, one originating in fissure in superior margin of orbit, another originating lateral to suborbital spine, both uniting above hepatic spine and disappearing posteriorly; a broad groove below and anterior to hepatic spine. Eyes moderately developed. Antennular peduncle with basal article hollowed out above, stylocerite broad, cupped longitudinally forming portion of socket for reception of eye, tip reaching nearly to end of article; second article of peduncle slightly shorter than third; inner flagellum hairy below, a little longer than antennal scale; outer flagellum shorter, smooth. Antennal scale broadest in posterior half, lamella tapering to narrow rounded tip; lateral border slightly convex; well-developed lateral spine exceeding lamella and as long as distal width of blade. Third maxilliped reaching nearly to tip of antennule; hairy.

First pair of legs strong, subchelate; hand less than 3.5 times as long as wide, palm with a strong spine at distal end of finger; merus with a small spine on lower margin. Second pair of legs almost filiform; minutely chelate, hand hairy. Third legs stronger; fourth and fifth normal.

Abdomen, viewed dorsally, tapering from broad first and second segments to narrow sixth segment. Telson slender, tapering; with four small spines above on lateral border, first pair at two-thirds length, second midway between these and acute tip; tip flanked by three pairs of movable spines, median pair longest and stoutest. Uropodal exopods with lateral border ending in a spine flanked medially by a longer movable spine.

Measurements.—Length of body: ovigerous females from North Carolina, 25 to 60 mm. Specimens from Delaware: males, to 47 mm.; females, to 70 mm. (Price, 1962).

Color.—Ash-gray with numerous irregular, stellate, blackish-brown spots or speckled with gray, imitating the color of sand; color subject to considerable variation in shade, tail often darker (various authors).

Habitat.—Usually near bottom over sand: low-water mark to 50 fathoms, rarely to 246 fathoms.

Type locality.—"Bay shores and inlets of the sea" [east coast of United States].

Known range.—Baffin Bay to east Florida; Arctic Alaska southward to Shumagin Islands, Alaska, and Ranshima, Hokkaido, Japan.

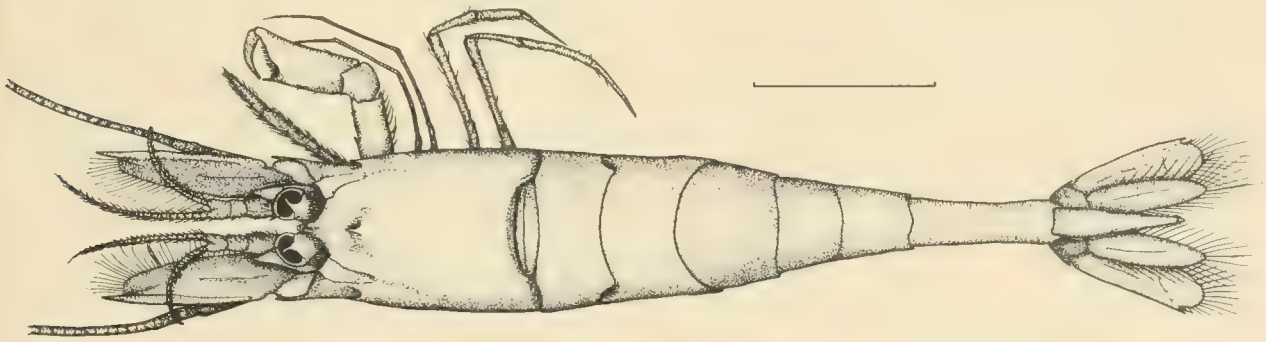

FIGURE 72.—*Crangon septemspinosa* Say. Ovigerous female in dorsal view, legs of left side not shown, 10 mm. indicated.

Remarks.—At the time of Hay and Shore's account, it was apparent that *C. septemspinosa*, with northern rather than southern affinities, fluctuates in abundance seasonally in estuaries near Beaufort, N.C. Ovigerous females have been found in North Carolina from December through May and in August and late fall (Hay and Shore, 1918, in part). Individuals taken in winter are larger than those found in spring. Juveniles have been found in this region from December to July, but from midsummer to late fall juveniles and adults disappear from estuaries.

Bigelow and Sears (1939) reported much the same pattern of occurrence in waters of the Continental Shelf from Cape Cod to Chesapeake Bay, with greatest occurrence in February dwindling to rare occurrence in July, but never abundant anywhere. They found the species limited, probably by depth and not by distance from shore, at about the 27-fathom curve, and remarked on probable importance of the species in the diet of predatory fishes. The role of the species in diets of fishes has long been recognized (Whitley, 1948).

On Georges Bank, where Whitley (1948) made all collections inside the 100-fathom curve, *C. septemspinosa* was most common in September and January, rarest in June, and usually occurred near the bottom. He reported maximum numbers in July at Woods Hole, and in August in the Bay of Fundy. Ovigerous females were found in spring and early summer. The species was judged to produce one brood a year and to have a life span of 1 year.

Price (1962), studying the biology of *C. septemspinosa* in Delaware Bay, made collections in a salinity range of 4.4 to 31.4‰ at temperature extremes of 0.0° to 26.0° C. Growth rate was estimated to be 1.6 mm. per month, with no observed seasonal variation in rate. The major breeding season was judged to be March to October, but ovigerous females were found throughout the year in salinities of 17.7 to 29.3‰, and temperatures of 0.0° to 25.0° C. First egg bearers of the year were found to be large females, with smaller ovigerous females more numerous in July. Females outnumbered the males, especially during the most active spawning season. At 21° C., eggs hatched after 6 or 7 days in the laboratory.

Contrary to the appraisal of other authors, Price judged that 3 year classes of females and 2 year classes of males occur in the shoal waters of Delaware Bay in spring. Food studies indicated a diet of planktonic crustacea and scavenged material. Sanders, Goudsmit, Mills, and Hampson (1962) found a diet of small bottom plants and animals.

Fish (1925) found the larvae appearing from February to May and as late as December at Woods Hole. Needler (1941) recorded hatching times from late spring to early summer (July) around Prince Edward Island, Canada. She described five larval stages and a postlarval stage. All these stages were obtained in July from plankton tows made about a meter below the surface along the shores of estuaries. Larvae were hatched in the laboratory, but the series of stages was worked out from plankton.

These data indicate an extended breeding season in high latitudes. Variations in seasonal abundance in different localities north of Chesapeake Bay are possibly the result in part of varied sampling methods in different years by different investigators.

Work on color control of *Crangon* and related species, too involved for appropriate summary here, has been reviewed by Kleinholz (1961).

Suborder **Reptantia**

Usually lobsterlike or crablike in form. Cephalothorax usually depressed. Rostrum usually small or absent, depressed if present. Antennules without stylocerite. Legs strong, first pair usually, but others never, stronger than remainder. Abdomen, whether well developed or greatly reduced, more or less depressed with first segment distinctly smaller than rest; pleopods often reduced or absent.

Section **Macrura**

Abdomen straight, symmetrical; usually well armored, with well-developed pleura and a strong tail fan (Schmitt, 1921).

Superfamily **Scyllaridea**

First article of antennule fused with epistome. Antennal scale absent. All legs nearly equal in length and none chelate except subchelate last pair in females. First abdominal segment without

pleopods; tail fan divided into a soft membranous and striated hinder part and a harder anterior portion.

Family **Palinuridae**

Carapace subcylindrical. Eyes not enclosed in separate orbits formed by edge of carapace. Antennae not flattened but furnished with large, long, rather rigid, multiarticulate, usually spinose flagellum.

The fossil record for the family Palinuridae extends back to the Cretaceous in North America (Rathbun, 1926, 1935).

Genus ***Panulirus*** White, 1847

White, 1847b, p. 69.—Hemming, 1958b, p. 174.

Panulirus argus (Latreille). Spiny lobster, crawfish

Figure 73

Palinurus argus Latreille, 1804, p. 393.
Panulirus argus: White, 1847b, p. 69.—Hay and Shore, 1918, p. 398, pl. 28, fig. 3 (rev.).—Crawford and deSmidt, 1922, p. 291, figs. 265–271.—Schmitt, 1935a, p. 172, fig. 36 (rev.).

Recognition characters.—Carapace covered with strong spines arranged more or less in regular longitudinal rows; spines above orbits very large, compressed, and curved upward and forward. Eyes large and prominent. Antennules nearly two-thirds length of body; peduncles slightly exceeding antennal peduncle; outer flagellum shorter and thicker than inner, and strongly ciliated distally. Antennal segment with a pair of spines in front, a weaker pair about halfway to eye, a strong median spine and weaker lateral spines below insertion of antennules. Antennae very large, heavy, exceeding body by more than length of carapace; peduncles with numerous strong spines; flagellum stout, stiff, a line of cilia along inner margin and ringed with spines at intervals.

Legs rather weak, tips acute and bristly; female possessing a small subchela on fifth legs with concave opposed surfaces formed between distal portion of propodus and proximal portion of dactyl.

Abdomen smooth, each segment crossed by a furrow more or less distinctly interrupted at middle; pleural angles each produced into a strong, sharp, backwardly directed tooth deeply notched and serrated on posterior margin. Pleopods absent from first segment of abdomen; exopod of pleopods broad, laminate; endopods missing in males, females with endopods of second pleopods laminate, last three endopods bifurcated. Proxi-

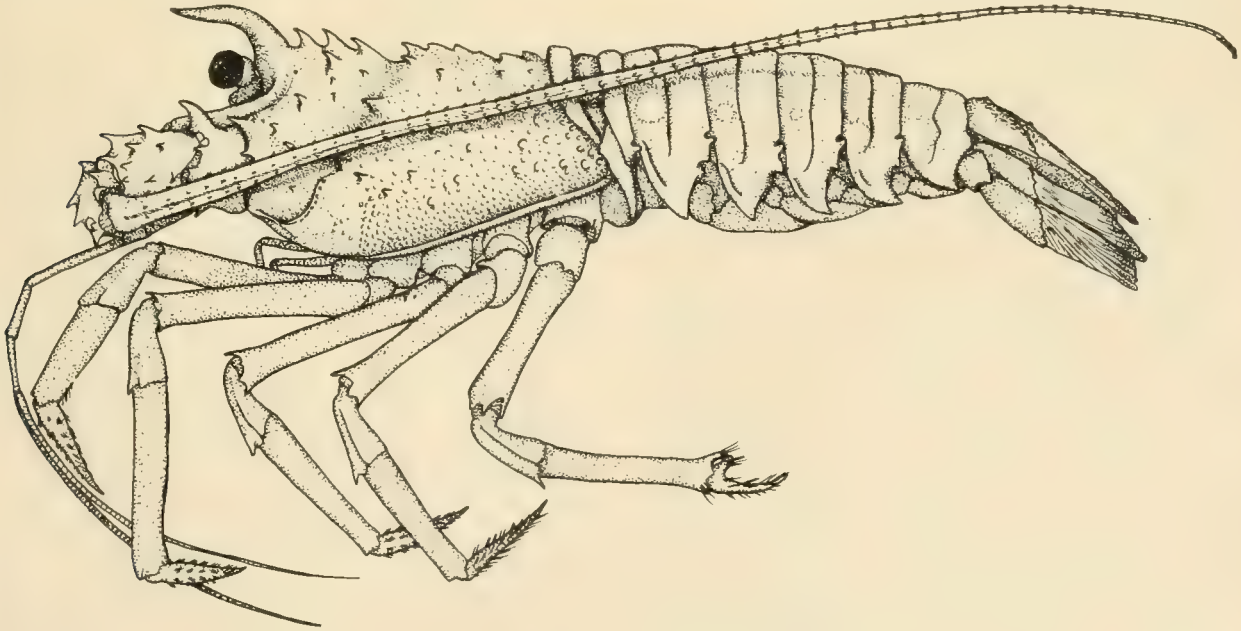

FIGURE 73.—*Panulirus argus* (Latreille). Female in lateral view, approximately × 0.5.

mal division of telson with rather strong spines; distal division with weak spines and cilia in longitudinal lines. Uropods hard proximally, membranous distally; basal article bispinose, a row of denticles along margin of hard part, and lines of minute spines and setae on upper surface of membranous part.

Measurements.—Length of body from orbit to tip of telson: to approximately 450 mm. (18 inches), occasionally larger.

Variations.—Aside from individual variations which will not be discussed here, the species exhibits marked allometric variations with age as well as sexual dimorphism. These features were discussed in detail by Crawford and deSmidt (1922) and are summarized here. Antennae of the young are longer in proportion to the body than in adults. Setae present on the young disappear in the adult and the sharpness of spines on the body tends to diminish with age, except for those on anterior portions of the carapace.

As pointed out in the description, only the females have chelate fifth legs. In adult males, the second pair of legs is extraordinarily developed. They are long, rarely used in walking, and the dactyl is long, curved, and provided with a brush of setae. The length of the dactyl, its curvature and setation increase with age. Sexual differences in the pleopods are given in the description.

Males have a relatively more inflated and longer carapace than females. Conversely, in females the abdomen represents a greater proportion of total length of the body than in males. Maximum lengths of the two sexes, however, are about the same (Creaser, 1952). The posterior margin of the sternum in males is narrower than the comparable structure in females and the sternum is longer.

Color.—Coloration largely separable into two groups, (1) lightly colored individuals ranging from light gray and tan to shades of green and light brown, and (2) darkly colored individuals varying from shades of red to deep brown and blue. Abdomen spotted with yellowish ocelli; posterior margin of each segment edged with yellow or orange, lower angles of segments marked with bluish or greenish tints and sometimes additional colors. Tail fan crossed by bands of orange, yellow, and black, fringed with white. Pleopods usually orange, about half of surface covered by a black blotch. Legs striped longitudinally with blue. Ventral surfaces of body light yellow; thoracic sternum marked with irregular radiating stripes.

Young with coloration of carapace arranged in transverse bands, usually three, middle one dark; antennae frequently ringed with alternate light and dark bands; legs ringed with blue (Crawford and deSmidt, 1922).

Habitat.—On reefs or among rocks, among growths of sponges or other objects which afford protection or places of concealment; low-tide mark to depths of about 50 fathoms. Experimentally, lobsters at Bermuda have withstood depths of 250 fathoms (Creaser and Travis, 1950).

Type locality.—Erroneously given as East Indies ("des Grandes-Indies").

Known range.—North Carolina through Gulf of Mexico and West Indies to Rio de Janeiro, Brazil; Bermuda.

Remarks.—A number of papers have been published concerning the general ecology of *Panulirus argus.* Only a summary of this work can be given here. The most comprehensive single, general treatment is that of Crawford and deSmidt (1922) for the species in Florida, but substantial additions to this work have been given by Dawson (1949, 1954), Dawson and Idyll (1951), Lewis (1951), Lewis, Moore, and Babis (1952), Marshall (1948), and Smith (1951). Mattox (1952) gave biological notes on the species in Puerto Rico, and Creaser (1950, 1952), Creaser and Travis (1950), and Sutcliffe (1952, 1953, 1957) discussed the species in Bermuda.

North Carolina must be regarded as the extreme northern edge of the range of this species, and, indeed, concentrations of the species large enough to be exploited commercially occur only in southern Florida, the West Indies southeast to Puerto Rico, and at Bermuda. A large population may exist in deep water in the northern Gulf of Mexico (Moore, 1962). Differences in growth rate and breeding habits may exist among these areas.

Panulirus argus grows to a large size. In its first year of life it reaches a length of about 2 inches (measurements of this species usually given in inches in U.S.A.) and, though growth in the young individuals is more rapid than in older animals, increments in length after that time are

about an inch a year. Adults of 16-inch length are approximately 16 years of age, the males attaining somewhat greater lengths than females.

After juvenile stages are past, molts average about 2½ times per year, occurring most frequently from March to July and from December to February, at least in the Florida area. Among captive animals, molts without growth can occur. About 12 days elapse from the first sign of molting until the new exoskeleton is hard enough to resist denting, though hardening of the new shell is not complete until the 28th day. Travis (1954, 1955a, 1955b, 1957) gave an exhaustive study of the molting process among spiny lobsters near the age of sexual maturity. This work is beyond the scope of the present summary, but her findings show that molting among captive adolescent animals is largely confined to the warmer months at Bermuda and is more frequent than among Florida specimens. Other evidence shows that growth of the young is more rapid in Bermuda than in Florida, and that sexual maturity is reached sooner.

The mating season in Florida is principally from March through July. Sexual maturity is reached in females as small as 6 inches long, but ovigerous females under 8 inches in length are rare. Mating pairs are judged to be about the same age, and mating usually occurs in the hard-shelled stage. At the time of mating the male places a waxy spermatophore on the thoracic sternum of the female. Prior to spawning, the female scratches the surface of this packet with the chelate fifth legs. The actual egg laying is accomplished in about one-half hour, during which the female lies partially on her back forming a trough of the underside of her abdomen with the aid of the exopods of the pleopods. Eggs extruded from the oviducts pass backward from the bases of the third legs over the spermatophore and become attached to the endopods of the last three pairs of pleopods. After spawning, the spermatophore appears eroded as if enzymatic action had partially destroyed it. The eggs hatch in about 1 month. A second mating and egg laying may ocur about a week after the hatch of the first batch and at this time the ovary is spent and the spermatophore almost completely eroded away. Molting of females during this season occurs only after spawning.

The spawning season in Florida is principally from March through June, and mostly in April. However, a few ovigerous females occur as late as October (December in the Bahamas). In Puerto Rico, the spawning season may be more extended than in Florida, for 22 percent of females in the commercial catch in Puerto Rico are ovigerous in September and 18 percent in October.

Direct evidence from the studies in Bermuda shows that females may lay eggs twice in a season. The number of eggs laid depends on the size of the individual, and the second brood is smaller than the first. Estimates show that a 9-inch female can lay 500,000 eggs, a 12-inch female 1,118,656, a 15-inch female 2,566,916. A second laying by a 13-inch female consisted of 1,008,788 eggs. Thus, it is estimated that a 15-inch female might lay 4 million eggs a season.

In Bermuda and elsewhere, there is apparently a movement of females from shallow to intermediate depths and from deeper water to these depths for spawning. Aside from these movements, there is evidence in Bermuda that the lobsters exhibit considerable homing tendencies, often moving as much as 5 miles against strong tides to return to the place of original capture. Adults tagged in Florida, on the other hand, have moved as much as 100 miles in 100 days (Smith, 1954), but such movement is probably exceptional.

The larva of the spiny lobster is a flattened, leaf-shaped, planktonic organism which, before its identity was known, was given the name phyllosoma. Development of the phyllosoma larvae of *P. argus* has been studied off Florida and at other points in the Atlantic Ocean from the West Indies to the southeastern coast of the United States and north of Bermuda. Bigelow and Sears (1939) found phyllosoma larvae (*P. argus?*) off Chincoteague Bay in July, 1929. Eleven stages have been described from plankton. In Florida, the bulk of freshly hatched larvae appear between June and August, the last stages being taken in December and January. The first postlarval, or puerulus, stages appear in inshore waters from January to March. Thus, larval development is judged to require 6 months, and during that time the larvae may be swept hundreds of miles from the spawning place. (Feliciano (1956) described a prenau-

pliosoma stage which may at times be freed in the water but this has yet to be confirmed.) The puerulus is shaped like a miniature adult, but is about 17 mm. long, colorless, and has a soft exoskeleton. It is nonplanktonic and settles in shallow water. Ten postlarval stages have been distinguished. Stages one through three avoid light, but later stages show no such reactions. At the end of the first year, at the eleventh postlarval stage, the young are approximately 2 inches long.

Aside from reactions of the very young postlarvae to light, Hess (1940) showed that freshly molted adults are sensitive to light in many regions of their bodies, but as soon as the body is again sclerotized no such reactions are apparent. Sutcliffe (1956) demonstrated that in clear, shallow water lobsters sought cover in bright moonlight. He concluded that movements attributed to tidal responses were actually responses to light.

Stridulation by spiny lobsters (Palinuridae) has been described by a number of workers (Moulton, 1957) and in *P. argus* it is produced primarily by a toothed ridge medial to the bases of the antennae and extending anteriorly from beneath each eye. A corrugated membrane at the base of each antenna is played against this ridge, producing sound when the membrane is moved proximally. Two types of sound are produced, a slow rattle normally produced by animals in small groups, and a rasp which accompanies defensive behavior. A squeaking sound is also produced in an unknown manner, by vibration of the body, when a specimen is held in the hand of an observer. The effect of these sounds on other lobsters or marine life is unknown.

Pearse (1932a) determined the freezing point of *P. argus* blood at Tortugas (range −1.86° to −2.39° C.).

Family **Scyllaridae.** Spanish lobsters

Carapace depressed; exoskeleton thick, hard, sculptured or tuberculate; orbits excavated in margins of dorsal surface. Antennae short and broad with flat scalelike, stiff articles. Mandibles with a one-jointed palp. Legs simple except minutely chelate fifth pair in female.

The fossil record for the family Scyllaridae extends back to the lower Eocene of the Gulf Coast in North America (Rathbun, 1935).

KEY TO GENERA AND SPECIES IN THE CAROLINAS

(Adapted in part from manuscript key by F. A. Chace, Jr.)

a. Exognath of outer maxillipeds without a flagellum; terminal article of antennae with edge cut into deep lobes distally ..... *Scyllarus* (p. 94).
  b. Prominences on carapace blunt; second article of antennular peduncles dorsally flattened; distal articles of antennae meeting, or nearly meeting, in midline; first four abdominal tergites obscurely notched posteriorly in midline; pleura of fourth abdominal segment rounded laterally.
    c. Pregastric tooth of carapace broadly rounded; two, seldom three, distinct parallel grooves between posterior marginal groove and posterior margin of carapace; first to fourth abdominal segments with notch in posterior margin very shallow; fourth abdominal segment not elevated in midline ..... *chacei* (p. 95).
    cc. Pregastric tooth almost always bilobed, incised; almost always a single distinct groove between posterior marginal groove and posterior margin of carapace; first to fourth abdominal segments showing a deep, narrow, median notch in posterior margin; fourth abdominal segment elevated, more or less ridgelike in midline ..... *americanus* (p. 96).
  bb. One gastric and all lateral prominences on carapace sharp; second article of antennular peduncles cylindrical; distal articles of antennae not nearly meeting in midline; first four abdominal tergites deeply and acutely notched posteriorly in midline; pleura of fourth abdominal segment sharply rectangular or acute laterally ..... *ncarctus* (p. 97).
aa. Exognath of outer maxillipeds with a flagellum; terminal article of antennae with edge nearly smooth or crenulate distally ..... *Scyllarides nodifer* (p. 98).

Genus ***Scyllarus*** Fabricius, 1775

Fabricius, 1775, p. 413.

Recognition characters.—Carapace flattened, width at anterolateral corners equal to or slightly greater than length in midline; middorsal ridge and an oblique ridge on each side prominent. Antennules with first articles broad, flattened, and immovable, second article much narrower and elongate; third and fourth articles slender; flagella short; abdomen, including telson, much longer (nearly twice) than carapace; pleura of first segment incised in center of lower edge, second broad and pointed distally. Anterior pleopods of male with both rami slender, flattened, hairy on outer border; remainder with exopods small and lamellate, endopods rudimentary. Anterior pleopods of female with both rami broad and flattened; exopods of remainder lamellate,

endopods slender and with long silky hairs. Legs stout, extending beyond carapace; first legs stoutest, remainder progressively more slender; second pair longest; dactyls of first pair somewhat serrate on lower border, remainder simple; fifth legs of females subchelate. Third maxillipeds stout, basal articles prismatic.

Scyllarus chacei Holthius

Figure 74

Scyllarus americanus: Hay and Shore, 1918, p. 399, pl. 28, fig. 2.—Bouvier, 1925 (in part), pp. 448–450, pl. 7, fig. 3.—Boone, 1930, p. 84, pl. 23, fig. A. Schmitt, 1935a (in part), p. 174, fig. 39.—Holthuis, 1959, p. 126.
Scyllarus chacei Holthuis, 1960b, p. 152.

Recognition characters.—Carapace with surface squamose in part dorsally, lightly squamose below lateral borders, with feathered setae (some darkened) between squames; middorsal ridge with anterior (pregastric) eminence large, rounded, gastric eminence higher, upturned, cardiac eminence somewhat smaller than pregastric; two coalesced spines over each orbit large and somewhat separated from ridges over branchial areas. Rostrum short, rounded, sides nearly parallel. Anterior border of carapace emarginate. Orbits deeply excavated with a broad anterior notch, a blunt tooth on proximal (fixed) antennal article in center of notch. Anterolateral corners of carapace spiniform, lateral borders roughened with squames; a rather deep notch behind orbit and another one farther back; area between posterior marginal groove and posterior margin of carapace nearly smooth but traversed by two, seldom three, distinct parallel grooves.

Second antennular article elongate, flattened above, anterior margin obliquely truncate. Antennae spatulate, somewhat punctate; distal article with irregularly rounded anterior border cut into seven elongate, somewhat separated, lobes with rounded ends, edges ciliated; medial two lobes shortest and sharpest, lateral lobe obliquely truncate and broadest; penultimate article short, bilobed in dorsal view; proximal movable article cordate, a prominent ridge throughout length to spiniform tip, a less conspicuous and irregularly shaped medial ridge, edges spinose.

Second, third, and fourth abdominal tergites (and to some extent first) with arborescent furrows running inward and forward toward midline; first to fourth segments with median notch in posterior margin very shallow, fourth segment not elevated in midline. Third to fifth pleura rounded distally, sixth with a rounded anterolateral lobe. Sternum triangular, broad at base, smooth with furrows ciliated; male with slight midventral elevation on fifth plate, elevation less evident in female.

FIGURE 74.—*Scyllarus chacei* Holthuis. Male in dorsal view, approximately × 2. Bob Simpson photo.

Measurements.—Length of carapace, 19 mm.; length of abdomen 35 mm.

Habitat.—Nine to 100 fathoms.

Type locality.—North-northwest mouth of Marowijne River, about 20 miles off coast of Surinam.

Known range.—Off Cape Lookout, N.C., through Gulf of Mexico, West Indies, and Caribbean Sea to off Cape São Roque, Brazil.

Remarks.—Ovigerous females have been taken off Florida in March, South Carolina in July, Surinam in August and September, and northeast Brazil in November.

Scyllarus americanus (Smith)

Figure 75

Arctus americanus Smith, 1869b, p. 119.
Scyllarus americanus: Bouvier, 1925 (in part), pp. 448–450.—Holthuis, 1960b, p. 152 (restr.).

Recognition characters.—Carapace with surface squamose in part dorsally, a little squamose below lateral borders posteriorly, lightly tuberculate toward epistome, with feathered setae (some darkened) between squames; middorsal ridge with anterior (pregastric) eminence large, bilobed anteriorly, gastric eminence sharper and more elevated, cardiac eminence not so sharp, bilobed; two coalesced blunt spines over each orbit large and somewhat separated from ridges over branchial areas. Rostrum short, rounded at tip, a blunt keellike middorsal tubercle above. Anterior border of carapace emarginate. Orbits deeply excavated, margins broad, with a broad anterior notch; a blunt tooth on proximal (fixed) antennal article in center of notch. Anterolateral corners of carapace spiniform, lateral borders roughened with squames; a rather deep notch behind orbit and another one farther back. Area between posterior marginal groove and posterior margin of carapace faintly squamose and traversed almost always by a single distinct groove.

Figure 75.—*Scyllarus americanus* (Smith). Ovigerous female in dorsal view, approximately × 1.5. Bob Simpson photo.

Second antennular article elongate, flattened above, anterior margin obliquely truncate. Antennae spatulate, somewhat punctate, surface variably covered with feathered setae; distal article with irregularly rounded anterior border cut into six somewhat separated lobes, edges ciliated, medial lobe short, spiniform, next much larger and less pointed, following three about equal in length, tips rounded, lateral lobe about twice width of intermediate lobes; penultimate article short, bilobed in dorsal view; proximal movable article triangular in outline, edges spinose, two lateral spines larger than four variably sized medial spines, a prominent ridge running to apical spine nearly dividing article in half.

Second, third, and fourth tergites of abdomen (and to some extent first) with arborescent furrows running inward and forward toward midline. First to fourth segments with median notch in posterior margin fairly deep and narrow; fourth segment elevated, more or less ridgelike in midline. Third to fifth pleura rounded distally, sixth with a narrowly rounded anterolateral lobe. Sternum triangular, broad at base; smooth with furrows ciliated; male with a low tubercle in center of fifth sternite, female similar.

Measurements.—Ovigerous female: length of carapace, 25 mm., width, 29 mm.; length of abdomen, 45 mm.

Habitat.—Surface to 19 fathoms, usually 3 to 12 fathoms.

Type locality.—Edgmont Key, Fla.

Known range.—Off Bogue Inlet, N.C., to southern Florida; Campeche Banks off Mexico.

Remarks.—Ovigerous females have been taken in southern Florida in September.

Scyllarus nearctus Holthuis

Figure 76

Scyllarus nearctus Holthuis, 1960b, p. 151.
Scyllarus arctus paradoxus: Rathbun, 1900b (in part), p. 309.

Recognition characters.—Carapace with surface squamose in part dorsally, but only on or near ridges and sides, smooth below except a sinuous submarginal row of tubercles and a lightly granulate area posteriorly, densely ciliate above between squames and on smooth areas. Rostrum short and acute; pregastric tooth above it about same size, gastric tooth larger, acute, all three of these directed forward. Cardiac eminence blunt, bilobed at apex. Gastric tooth and cardiac eminence with squames at base, rostrum and pregastric tooth in smooth area. Lateral ridges ending anteriorly in a forwardly directed spine. Front emarginate with a small projection about halfway between rostrum and orbit. Orbits deeply excavated, upper border composed of two spines coalesced at base, lower border an inflated ridge more or less interrupted by two subequal spines at anterolateral corner; anterior notch partially occupied in middle by a large serrulate tooth on first (fused) antennular article and another eminence forming articulation of second antennal article. Anterolateral corners of carapace drawn out to a strong spine, lateral border with a notch behind eye and another less definite notch behind anterior end of branchial ridge. Posterior margin of carapace with a sharp but broadly opened notch in midline; area between posterior marginal groove and posterior margin of carapace traversed by two rows of squames.

Anterior border of first antennular article with low teeth or irregularities; second article cylindrical with a flattened, rounded distal projection; succeeding articles slender, flagella short. Antennae spatulate, fairly smooth, ciliated, edges densely covered with longer feathered setae; distal article semielliptical in outline, edge broken into six well-separated lobes with narrowly rounded tips, inner lobe smallest, outer broadest and subtruncate, a suggestion of a seventh lobe medially; penultimate article short, irregularly spined and lobed; first movable article roughly triangular with apex formed by a strong spine, two spines on outer border and three spines on inner border, apical spine and first two inner spines with small spurs on medial borders, third spine at mediopposterior border smaller, a definite ridge running across article from articulation to apex.

Second to fifth abdominal segments (and to some extent first) with arborescent furrows running inward and forward toward midline. First to fourth segments with median notch in posterior margin deep and narrow. Third and fourth with distal edge of pleura rounded anteroventrally, angled at posteroventral corner; fifth broadly rounded distally; sixth with anteroventral lobe broad and rounded. Telson with four flattened spines at distal edge of hard portion. Each ramus of uropods with a spine at same level on outer margin.

FIGURE 76.—*Scyllarus nearctus* Holthuis. Male paratype in dorsal view, approximately × 1.5. Bob Simpson photo.

Sternum triangular, narrower in males than in females, smooth, a little pubescent in grooves. Male with a strong, shelflike protuberance on sternite between last pair of legs, and with a strong sharply ridged shoulder extending over genital pore. Female with a low eminence on sternite between last pair of legs.

Measurements.—Ovigerous female: length of carapace, 24 mm., width, 26 mm.; abdomen, length, approximately 50 mm.

Habitat.—Thirty to 100 fathoms.

Type locality.—South of Dry Tortugas, Fla.

Known range.—Off Cape Hatteras, N.C., through Gulf of Mexico and West Indies to State of São Paulo, Brazil.

Remarks.—Ovigerous females have been taken off North Carolina in June.

Genus *Scyllarides* Gill, 1898

Gill, 1898, p. 99.—Verill, 1922, p. 18. (rev.).—Hemming, 1958b, p. 94.

Scyllarides nodifer (Stimpson)

Figure 77

Scyllarus nodifer Stimpson, 1866, p. 48.—Stimpson, 1871b, p. 123.
Scyllarides americanus Verrill, 1922, p. 24, pls. 5–6.
Scyllarides nodifer: Holthuis, 1960b, p. 153.

Recognition characters.—Carapace longer than wide, subtruncate in front, coarsely and unevenly granulate, granules elevated, not crowded, each surrounded by more or less complete circle of stiff hairs; anterolateral corners forming nearly a right angle terminating in an obtuse tooth; cervical notch and groove well marked with numerous denticles on margin in front of and behind notch; posterior transverse groove deep and conspicuous; gastric area with a large, broad-based, prominent median ridge divided into a smaller anterior and larger posterior part, each portion ending in an anterior, large, conical, obtuse or bilobed tubercle with other similar but smaller tubercles and coarse granules around and behind apex; cardiac region with a prominent but less elevated area with larger tubercles than on adjacent surface; a similar ridge on each branchial area. Orbits large, with prominent, thick borders, anterior notch wide and deep.

Antennae with distal article broader than long, edges broadly and evenly rounded, minutely lobulate and crenulate, fringed with short, close hairs; exposed portion forming a half oval, upper side covered with small, rough granules and small pits bearing tufts of short hairs in large adults, smoother in small individuals. Penultimate movable article showing two lobes beneath. Second movable article distinctly wider than long, broader than distal article; distal lobe terminating in nearly right angled point in large adults, armed with a spine in smaller specimens; edges dentate with many small teeth and some larger ones, a larger stout tooth near inner curve of inner margin; inner lateral lobe stout, thick, enlarged toward end; inner edges of these lobes of both antennae separated by a space about equal to orbit of eye. First movable article irregularly four-lobed above; small outer lateral lobe with about three denticles; median or distal lobe swollen and coarsely granular; inner lobe obliquely oblong with inner edge truncate and denticulate; prefrontal or rostral lobe a little broader than long, widest distally, swollen laterally, with concave sides and a median groove.

Outer maxillipeds large, basal articles stout. Legs projecting beyond carapace; first pair stouter than others, propodus considerably swollen, dactyl stout; fifth pair with propodus most slender; merus and carpus of all pairs, except carpus of first, with a finely serrulate carina ending in a sharp distal tooth; carpi, except first, with a lateral carina ending in a distal tooth; meri of last four legs with a ventrolateral carina ending in a sharp spine distally (carina sharpest on legs three and four) and each with a blunter medial spine distally.

Underside of bases of legs and sternum roughly sculptured, one larger acute or pyramidal elevation on sternum opposite base of each leg.

Abdomen strongly sculptured, elevated areas coarsely granulated and hairy, much like carapace. Second to fourth segments with a median, elevated, obtuse ridge, covered with large granules; fifth segment with slight ridge. Pleura large, angular; that of second segment largest, subacute, both edges with dentations about as large as adjacent granules; those of third to sixth segments more minutely dentate on posterior border, nearly smooth or minutely crenulate on anterior border. Telson broader than long, subtruncate distally; posterolateral angles broadly rounded; granulated and hairy proximally, covered with numerous forked ridges and grooves

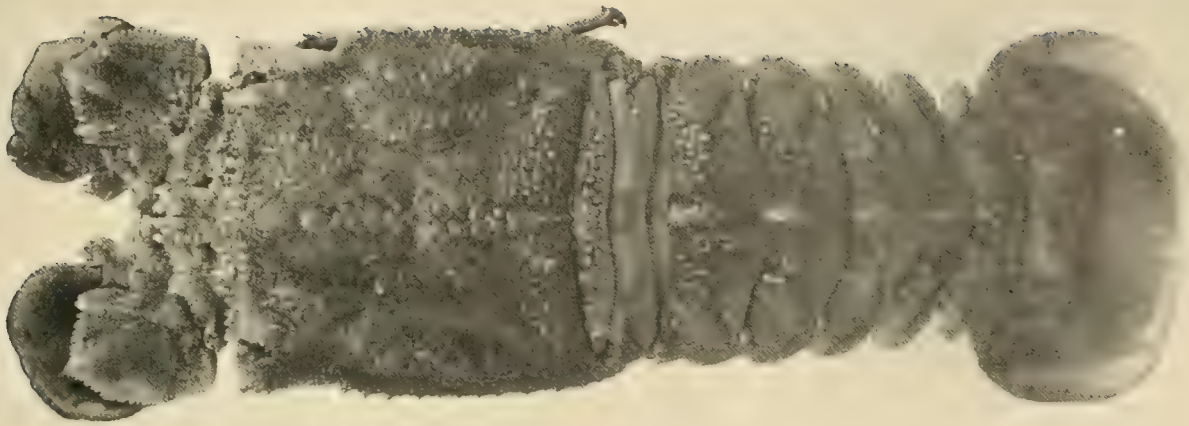

FIGURE 77.—*Scyllarides nodifer* (Stimpson). Female in dorsal view, approximately × 0.5. Bob Simpson photo.

distally becoming fine near edge. Uropods broad, sculptured as telson. Sternum of second segment in males bearing a sharply raised, serrate, heavily sclerotized ridge.

Measurements.—Length of carapace: female, 127 mm. Larger specimens have been observed but not measured.

Variations.—Smaller specimens are smoother than adults.

Color.—Body covered with irregular small brown spots on a grayish brown to yellowish background; many orange-red tubercles on edges, across ridge near rear edge of carapace, base and edges of antennal lobes; darker red spots at sides of gastric region, on anterior lobes of carapace and at middle of first abdominal segment; underparts yellow with darker yellow and brown spots; legs banded with red and purple; flagella of antennules purple.

Habitat.—Mud, shell, coral, and sandy bottoms; 16 to 40 fathoms.

Type locality.—Florida Keys.

Known range.—Bermuda; Cape Lookout, N.C., to Cuba; off Pensacola, Fla.

Remarks.—Little is known of these lobsters. They are sometimes used for food or bait.

Superfamily **Thalassinidea**

Exoskeleton often more or less membranous. Carapace compressed. Last articles of second to fourth legs not curved and flattened. Abdomen large, symmetrical, extended, sometimes with well-developed pleura; appendages of sixth segment usually adapted for swimming.

Family **Callianassidae**

Body shrimplike. Carapace with a "*linea thalassinica.*" Antennal peduncle five-jointed;

antennal scale vestigial, no antennal acicle. First pair of legs unequal or subequal, perfectly or imperfectly chelate; third and fourth pairs simple; others variable. Abdomen extended; pleura small or absent; sixth abdominal appendages with no sutures; tail fan well developed; broad appendages on third to sixth abdominal segments (after Hay and Shore, 1918; Schmitt, 1921).

KEY TO GENERA AND SPECIES IN THE CAROLINAS

a. Rostrum small; first two pairs of pleopods different from following three pairs; chelipeds dissimilar and unequal ..... *Callianassa* (p. 100).
b. Uropodal endopods narrow, about 4 times longer than broad ..... *C. major* (p. 100).
bb. Uropodal endopods not much longer than broad *C. atlantica* (p. 102).
aa. Rostrum large; second pair of pleopods like following three pairs; chelipeds alike and subsequal *Upogebia affinis* (p. 103).

Genus *Callianassa* [Leach, 1814]

Leach, [1814], p. 400.—Hemming, 1958b, p. 142.

The genus *Callianassa* has a fossil record extending back to the Jurassic (Rathbun, 1926).

Subgenus *Callichirus* Stimpson, 1866

Stimpson, 1866, p. 47.

Callianassa (Callichirus) major Say

Figure 78

Callianassa major Say, 1818, p. 238.—Schmitt, 1935b (rev.).
Callichirus major: Hay and Shore, 1918, p. 407, pl. 29, fig. 10.—de Man, 1928, p. 30 (rev.).

Recognition characters.—Integument more or less thin and membranous; chelipeds and an oval plate covering anterior three-fourths of carapace, being most hardened portions. Rostrum minute, somewhat obtuse; a similar projecting lobe at each side on margin of front. Cornea of eyes minute, situated at about middle of outer margin of flattened and pointed ocular peduncles. Antennular peduncles about two-thirds as long as carapace, stout, densely hairy below; each with two flagella about as long as distal article of peduncle. Antenna slender, longer than carapace, peduncle bent between second and third article.

Chelipeds unequal, showing sexual dimorphism. Males with major cheliped rather large; granular along proximal lower edge of carpus, lower edge of merus and over entire ischium; propodus and carpus about equal in length, twice as broad as merus and more than three times as broad as ischium; merus with a strong tooth on lower proximal border; fingers strong, dactyl hooking over outside fixed finger, a strong tooth near base. Major cheliped of female weaker, not granular; propodus and carpus proportionately shorter than in male; merus without tooth on lower proximal border; dactyl hooking over inside fixed finger. Minor cheliped of male and female similar, small; fingers weak, meeting only at tips; carpus as long as hand and somewhat wider. Chelipeds and first three pairs of walking legs much compressed; margins of distal articles on first two pairs especially sharp; first walking legs chelate, with long cilia on lower margin; second legs with propodus transverse, it and small triangular dactyl densely ciliate; third and fourth walking legs with last two articles hairy, last legs subcylindrical.

Abdomen long, gradually widening from anterior end to third segment, then narrowing

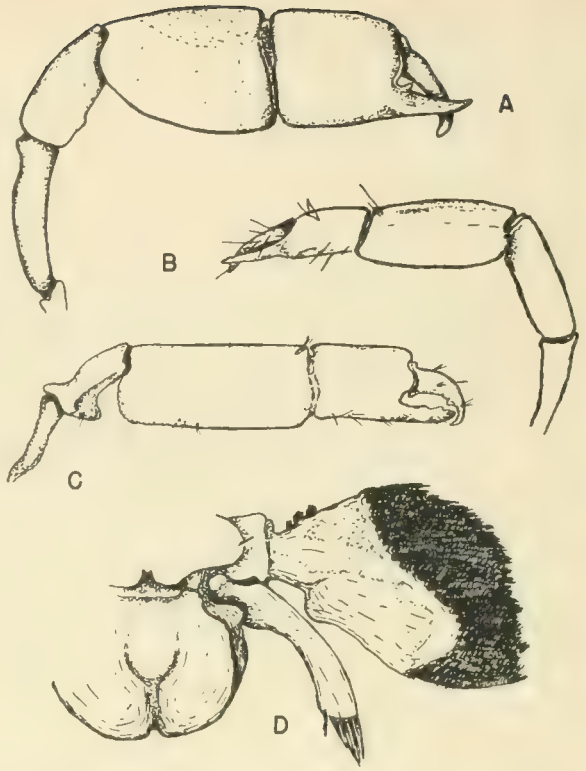

FIGURE 78.—*Callianassa (Callichirus) major* Say. A, major cheliped of female, approximately × 2; B, minor cheliped of male, approximately × 2; C, major cheliped of male, approximately life size; D, right uropod and portion of telson in dorsal view, approximately × 3 (after Lunz, 1937b).

slightly to sixth; sixth segment deeply grooved above. First two pleopods small and slender in male, larger and definitely biramous in female; remaining pleopods broad and overlapping. Uropods with exopod broad, rounded distally; distal half covered with mat of dense short hair becoming longer on border; endopod narrow, obliquely truncate, hairy at tip only. Telson with an inflated area on each side giving notched or fissured appearance.

Measurements.—Length of body: males, 95 mm.; females, 92 mm.; ovigerous females, 80 mm. (Lunz, 1937b).

Color.—Transparent gray except for porcelain white chelipeds and hardened portion of carapace (Lunz, 1937b).

Habitat.—Burrows in sandy shores on or near open ocean; intertidal zone to 1 fathom.

Type locality.—Coasts of Southern States and east Florida [St. Johns River].

Known range.—Beaufort Inlet, N.C., to eastern Florida; Grand Terre Island to Timbalier Island, La.

Remarks.—For many years this species was known only from a single specimen from Beaufort, N.C., and early descriptions of specimens from South Carolina and Florida. The rarity of occurrence in collections is due to the secretive burrowing habits of the form, for it easily escapes detection of the casual observer using conventional methods of collection. (Collections can be made by removing the mouth of the burrow, dropping pebbles or debris down the hole, waiting for the animal to appear at the exposed surface, then jabbing a shovel into the sand below the animal, thus cutting off escape into the burrow.) Such habits no doubt also enhance chances for fossilization, for the genus is abundant in the Cretaceous and Eocene of the Gulf coastal plain, and somewhat less abundant in later deposits down to the present time (Rathbun, 1935).

Lunz (1937b) was the first recent student to determine the habitat and abundance of the species in South Carolina and his studies were closely followed by those of Willis (1942) in Louisiana, and Pearse, Humm, and Wharton (1942), and Pohl (1946) in North Carolina.

The animal lives in deep burrows on sandy beaches that either face the open ocean or are close to it. In Louisiana, the burrows occupy a band from the intertidal zone to a distance of over 100 feet from shore in 5 to 6 feet of water. The tubular burrows, usually vertical to the surface, are divided into three portions. The mouth, about 5 mm. in diameter, opens into the upper portion, 5 to 20 cm. long and 5 to 8 mm. in diameter. From this the middle portion, 10 to 15 cm. long and often angled, widens gradually to approximately 20 mm. The third portion, 20 mm. wide, is the longest. An approximate average depth of the whole burrow is 146 cm. with variations from 60 to over 210 cm. Branches are common and arise most often from the middle portion. Characteristically, the burrows are lined with a brown material, thinnest in the upper portion and thickest (3 to 7 mm.) in the lower portion. The burrows often end in an enlarged pocket lined with crushed shell, and in some the lined tube extends below the pocket.

Burrow mouths are often surrounded by fecal pellets of *C. major*, which resist rapid disintegration in water. On some South Carolina beaches, such pellets were washed together in patches measuring up to 10 by 50 feet and piled to a depth of 0.25 inch. Mouths of burrows are not uniformly scattered but tend to be clumped in patches or tracts, often as dense as three or four openings per square foot. Chimneylike structures at the mouths of burrows noted by Say have not been confirmed, but a small raised ridge of sand often surrounds burrow mouths. Other mouths are not marked or may be located in a depression.

In captivity, the animals burrow in sand headfirst with the anterior appendages until a shallow pit is constructed, then the animals reverse themselves and continue to burrow tailfirst. Though the shrimp do at times emerge voluntarily from their burrows, such behavior is probably infrequent and may be confined to the breeding season (Lunz, 1937b). The species is well fitted for a fossorial life by virtue of the slender, elongate body, thin exoskeleton, and flattened hairy appendages adapted for burrowing, carrying sand, sifting food, and pumping water for feeding and respiratory currents. Examination of gut contents has shown an amorphous mass containing sand grains, diatoms and other algae, and many bacteria.

Ovigerous females have been reported from South Carolina in July and August, and they are

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known from North Carolina in June and July. Pohl (1946) counted 8,170 attached eggs on one female. *Pinnixa cristata* has been found as a commensal in the burrows.

Callianassa (Callichirus) atlantica Rathbun

Figure 79

Callianassa stimpsoni Smith, 1873c, p. 549, pl. 2, fig. 8.—Hay and Shore, 1918, p. 406, pl. 29, fig. 5.

Callianassa atlantica Rathbun, 1926, p. 107.—de Man, 1928, p. 37 (rev.).—Rathbun, 1935, p. 104.—Schmitt, 1935b, p. 4.

Recognition characters.—Integument smooth, shining, thin, almost membranous. Carapace about one-third length of abdomen, thin but with oval thickened plate on gastric region. Rostrum small, acute, flanked by a small triangular prominence at each side on frontal margin. Eyestalks small, flat, contiguous medially; pointed tips slender, curved outward and upward; cornea small, situated on outer border. Antennular peduncles about one-half length of carapace; flagella about as long as distal article of peduncle, densely hairy below. Antenna slender, longer than carapace; peduncle much shorter than that of antennules, bent between second and third articles. Third maxilliped operculiform; dactyl slender.

Chelipeds unequal, showing sexual dimorphism. Larger cheliped of male with fingers about equal in length, hairy, tips incurved; cutting edge of dactyl with a long, low, truncate tooth at base, smaller teeth distally; immovable finger with small teeth; palm hairy below, upper border ridged along proximal two-thirds; carpus as wide as but shorter than palm, upper and lower border ridged; merus articulating with carpus by extreme upper angle, a prominent, denticulate tooth on lower border proximally; ischium with six or seven subacute teeth on lower border. Smaller cheliped of male with fingers a little longer than palm; carpus four times as long as broad distally, a little longer than palm, half again as long as merus; merus twice as broad as long. Larger cheliped of female less toothed than in male; smaller cheliped as in male.

Abdomen with third to fifth segments of about equal width, each with a small patch of fine hairs on posterolateral angle; sixth segment broader than long. Male with no pleopods on first and second segments. Female with uniramous pleopods on first segment; slender, biramous pleopods on second segment; remainder well developed in both sexes. Telson nearly as long as broad; subtruncate distally, corners rounded. Exopods of uropods broader than endopods, both rami densely fringed with hairs distally.

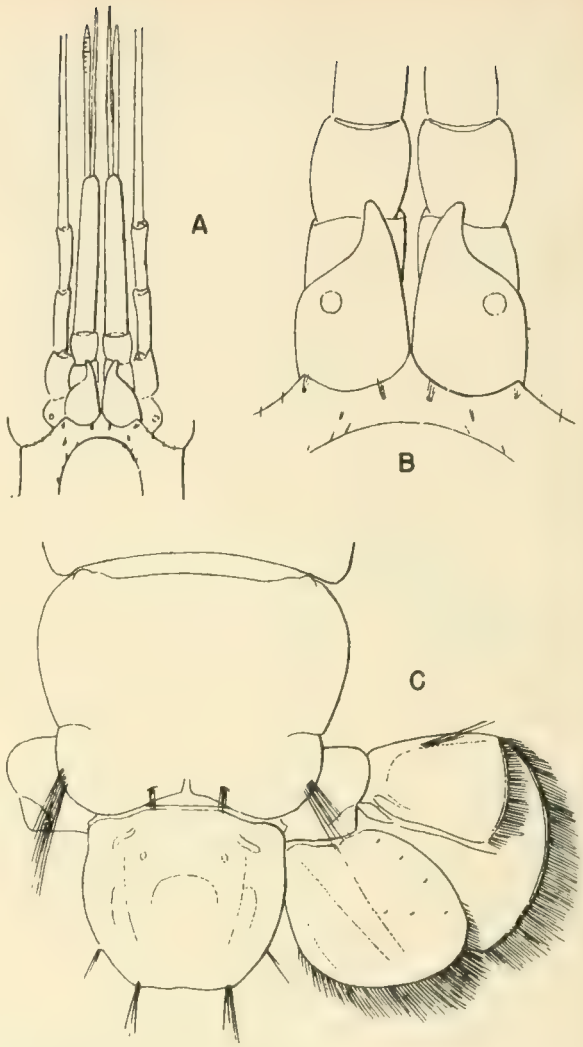

FIGURE 79.—*Callianassa (Callichirus) atlantica* Rathbun. A, frontal region in dorsal view; B, frontal region, eyestalks and antennules in dorsal view; C, sixth abdominal segment, right uropod and telson in dorsal view (after de Man, 1928).

Measurements.—Length of body: male, 59 mm.; female, 68 mm.

Habitat.—Muddy shores and bottoms in shallow water (Sumner, Osburn, and Cole, 1913a, b); shoreline to approximately 21 fathoms.

Type locality.—"Our species ranges from the coast of the Southern [United] States north to Long Island Sound" (Smith, 1873c).

Known range.—Bass River, Nova Scotia, to South Carolina; Franklin County, Fla.

Remarks.—Both de Man (1928) and Schmitt (1935b) pointed out that Rathbun renamed this species because the name *stimpsoni* was preoccupied by a fossil species of *Callianassa* named by Gabb in 1864. *Callianassa atlantica* itself has a fossil record extending from a first appearance in the upper Miocene of North Carolina and Virginia, and a later occurrence in the Pleistocene of Maryland to the present (Rathbun, 1935).

Ovigerous females have been taken in Massachusetts and South Carolina in July. Juveniles 4 mm. long have been collected on the surface in September in Massachusetts (de Man, 1928). This form is rarely taken in the Carolinas but has been collected in areas ranging from salty estuaries to offshore fishing banks.

Genus *Upogebia* [Leach, 1814]

Leach, [1814], p. 400.—Hemming, 1958b, p. 143.

Upogebia affinis (Say)

Figure 80

Gebia affinis Say, 1818, p. 241.
Upogebia affinis: Hay and Shore, 1918, p. 408, pl. 29, fig. 9.—Schmitt, 1935a, p. 196 (rev.).

Recognition characters.—Integument, except dorsal part of carapace and of legs, more or less membranous. Carapace about half as long as abdomen; cephalic portion about twice as long as thoracic, nearly flat above, anteriorly rugose and covered with short, rigid hairs. Rostrum large, flanked on each side at base by a large spine, spiny beneath in midline. A small upcurved spine behind eye on anterior margin, and a minute lateral spine behind cervical groove. Eyestalks concealed, pubescent above; corneal surface small. Antenna a little less than twice as long as carapace.

Chelipeds stout, a fringe of long hairs below; hands with an external, dentate ridge above, a median row of acute spines and an internal line of stiff hairs; immovable finger curved, movable finger much longer, denticulate above at base, cutting edges of both toothed near base; carpus grooved on outer face with a row of small spines and a strong marginal spine below, a row of small teeth on inner margin, and six acute spines along distal margin above; merus with a small spine above and a row of spines beneath. First pair of walking legs hairy at tips and along lower margin; merus with a strong spine at base. Remaining legs hairy at tips.

Abdomen gradually increasing in width from first to fourth segment, fifth narrower posteriorly, sixth subquadrate; lateral portions of third and fourth segments densely pubescent and all with pleura marked off by an impressed line. Tail fan densely hairy distally. Uropodal endopods truncate and with a median rib and costate outer border; exopods rounded distally and with two ridges. Telson broad, subquadrate, with an impressed median line.

Measurements.—Length of body: males, 61 mm.; females, 63 mm.

Variations.—Schmitt (1935b) mentioned the variability in spination of the lower border of the rostrum and multiple spination or lack of spines behind the cervical groove. Young specimens often lack these spines.

Color.—Gray, blue, or yellowish gray dorsally, tinged with light blue medially on tail fan and on fifth segment of abdomen, interlaced with uniform light lines; an oblique blue spot on side of

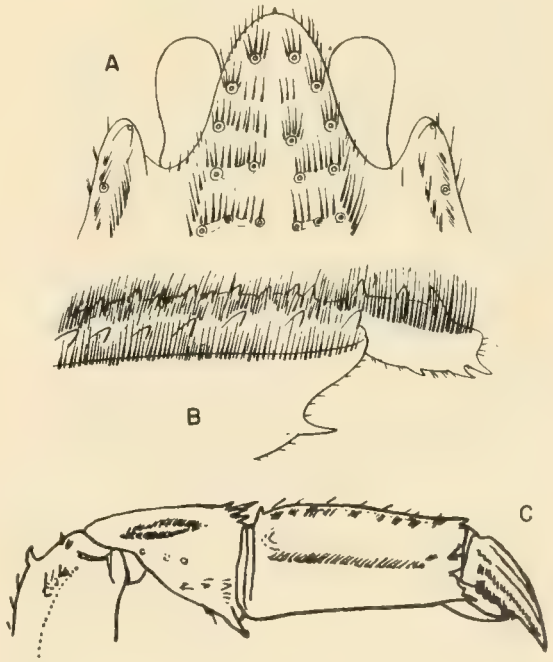

FIGURE 80.—*Upogebia affinis* (Say). A, rostral region and eyes of semiadult female in dorsal view; B, rostral region of semiadult female in lateral view; C, major chela (after de Man, 1927).

carapace at base of antenna extending posterodorsally; underparts light (various authors).

Habitat.—Burrows on estuarine mud flats and in shallow estuaries; intertidal to 15 fathoms.

Type locality.—Georgia.

Known range.—Wellfleet, Mass., to Rockport, Tex. (Hedgpeth, 1950); through West Indies to Maceió, Alagoas, Brazil (de Man, 1927).

Remarks.—A species of *Upogebia* is known from the Eocene of Alabama (Rathbun, 1935).

Ecological notes on *U. affinis* in North Carolina were reported by Pearse (1945). The species inhabits muddy situations in estuaries where salinities are fairly high. Its burrowing habits are similar to those of *Callianassa*. Wass (1955) found burrows prevalent in Florida where the marine grass *Halodule wrightii* stabilizes muddy substrates. Burrows examined by Pearse were 30 to 50 cm. deep with openings about 30 cm. above low-tide mark. They were often branched, containing several individuals each in its own branch, and showed one to eight small openings at the surface. In communal burrows he often found two or three ovigerous females and one or two juveniles. Like the burrows of *Callianassa*, those of *U. affinis* are narrowest in the upper portion. Pearse concluded that the animals seldom leave their confines.

In captivity, *U. affinis* made only feeble attempts to burrow. In nature, however, the animals are active and pump water vigorously from the anterior to posterior end of the body by flapping movements of the pleopods. Food is apparently strained from the water by the hairy mouth parts and walking legs, and probably consists largely of organic materials swept in the water current.

Ovigerous females were studied in detail in August, though Hay and Shore (1918) pointed out that the breeding season lasts throughout the summer, and juveniles have been collected in Bogue Sound, N.C., in plankton tows from early April to late October. Fish (1925) reported larvae at Woods Hole from mid-July to the latter part of October, but they were most abundant in early August. A single female may produce about 10,000 eggs at a time. They are borne on the first four pairs of pleopods. In captivity, more zoeae were hatched at night than in daytime. Pearse cited MacGinitie (1934) for evidence that *U. affinis*, like members of the related genus *Callianassa*, may live several years, though there is no evidence supporting this idea for the former.

Upogebia affinis is commonly parasitized in North Carolina by the bopyrid, *Pseudodione upogebiae* Hay. Pearse (1952a) described a parasitic isopod, *Phyllodurus robustus*, from a Florida specimen.

Section **Anomura**

Abdomen well developed, either symmetrical and flexed beneath thorax, exceptionally extended in a straight line usually flexed on itself, or asymmetrical, coiled and imperfectly armored, almost always with biramous appendages on sixth segment. Carapace usually depressed, free from epistome, traversed on either side in longitudinal or obliquely longitudinal direction by distinct suture (*linea anomurica*) more or less marking off sidewall of carapace from dorsal and dorsolateral portion. Last thoracic sternum free (or atrophied). First pair of legs well developed and chelate; second and third pairs well developed, not chelate; fifth pair markedly different from third.

Superfamily **Galatheidea**

Carapace more or less depressed. Abdomen relatively well developed, not closely folded beneath cephalothorax, symmetrical, and with well-developed pleura, but to some extent not capable of complete extension. Eye scales absent. Antennal peduncle with third article indistinct. Last thoracic sternum distinct. Second to fourth legs with dactyl not curved and flattened. Males with at least a pair of sexual appendages.

Family **Galatheidae**

Carapace longer than wide, often ornamented with transverse, ciliated lines. Rostrum distinct and strongly pointed, projecting beyond eyes. Antennular peduncle elongate. Antennae with four-jointed peduncle. Chelipeds greatly elongated, slender. First, second, and third walking legs well developed; fourth leg feeble, reduced in size. Abdomen bent upon itself but not folded under thorax; males with a pair of sexually modified pleopods on segment two, a pair of uniramous pleopods on segments three, four, and five; females with rudimentary pleopods on second abdominal segment, fully developed pleopods on three, four, and five.

KEY TO GENERA AND SPECIES IN THE CAROLINAS

a. Rostrum rather broad, margins toothed
Galathea rostrata (p. 105).

aa. Rostrum slender, toothless except for supraocular teeth at extreme base *Munida irrasa* (p. 105).

Genus *Galathea* Fabricius, 1793

Fabricius, 1793, p. 471.—Milne Edwards and Bouvier, 1897, p. 13.—Hemming, 1958b, p. 143.

Galathea rostrata Milne Edwards

Figure 81

Galathea rostrata Milne Edwards, 1880, p. 47.—Hay and Shore, 1918, p. 402, pl. 29, fig. 4 (rev.).—Chace, 1942, p. 30.

Recognition characters.—Carapace somewhat flattened; transverse ciliated ridges prominent, at least four continuous for entire width of carapace; lateral margins with a number of acute spines. Front prolonged into a broad, acute rostrum armed with four strong, anteriorly pointing spines on each side. Third maxilliped with inner margin of merus armed with three or four spines.

Chelipeds nearly twice as long as body, comparatively heavy; with rows of spines or spiniform granules along margins and appressed, squamiform, ciliated granules on surfaces; a few larger spines on carpus and distal end of merus; hand a little shorter than body; fingers gaping at base.

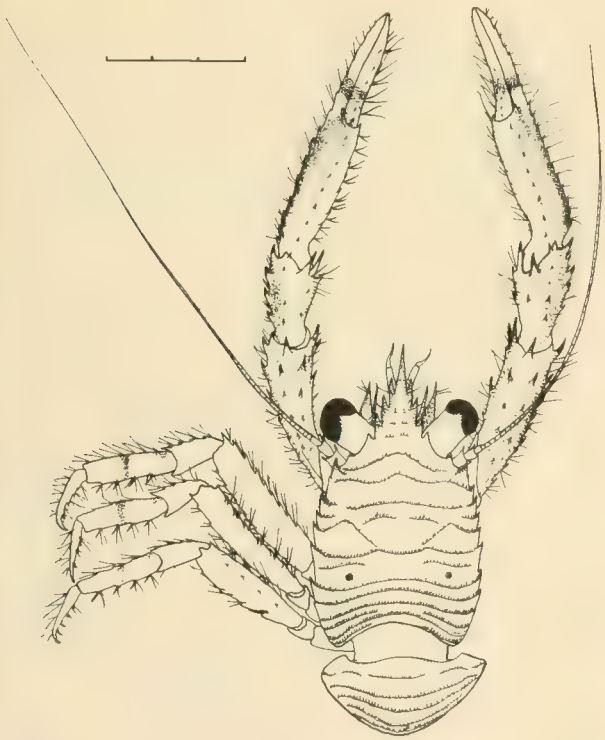

FIGURE 81.—*Galathea rostrata* Milne Edwards. Animal in dorsal view, walking legs of right side not shown, 3 mm. indicated.

Abdomen with transverse striae like those on carapace but without spines.

Measurements.—Length of body: male, 18 mm.

Color.—Ground color off white, cream, and light yellow; mottled with orange and reddish orange especially on legs, less evident on body; spines red or tipped with red; a single small circular reddish spot in center of each branchial region; a white band on propodi of walking legs; distal half of fingers white (from specimen recently preserved in formalin).

Habitat.—Ten to 50 fathoms; (rarely to 1,178 fathoms south of Block Island, R.I.?).

Type locality.—Sixteen miles north of Jolbos Islands [Yucatan Peninsula] at 14 fathoms.

Known range.—Off Cape Hatteras, N.C., to off Mississippi River Delta, and Yucatan, Mexico; (Rhode Island?).

Remarks.—Reports of this species are rare in the literature and only a few specimens have been taken off Beaufort, N.C.

Ovigerous females have been reported off western Florida in March and April (Milne Edwards and Bouvier, 1897, and U.S. National Museum records).

Genus *Munida* Leach, 1820

Leach, 1820, p. 52.—Milne Edwards and Bouvier, 1897, p. 20 (rev.).

Munida irrasa Milne Edwards

Figure 82

Munida irrasa Milne Edwards, 1880, p. 49.—Hay and Shore, 1918, p. 402, pl. 28, fig. 8.—Chace, 1942, p. 46 (rev.).

Recognition characters.—Carapace narrowed anteriorly, adorned with iridescent pubescence, spiny. Rostral spine much longer than supraocular spines, latter not extending so far as cornea. A row of 10 spines across gastric region in addition to 1 or 2 on each hepatic region, 2 to 4 on each triangular area, and 1 to 4 on either side behind cervical groove on inner portion of each branchial region; anterolateral spine long, followed by 6 distinct lateral spines. Merus of third maxillipeds with three spines on lower margin.

Chelipeds three or four times as long as carapace, covered with squamiform, ciliated tubercles;

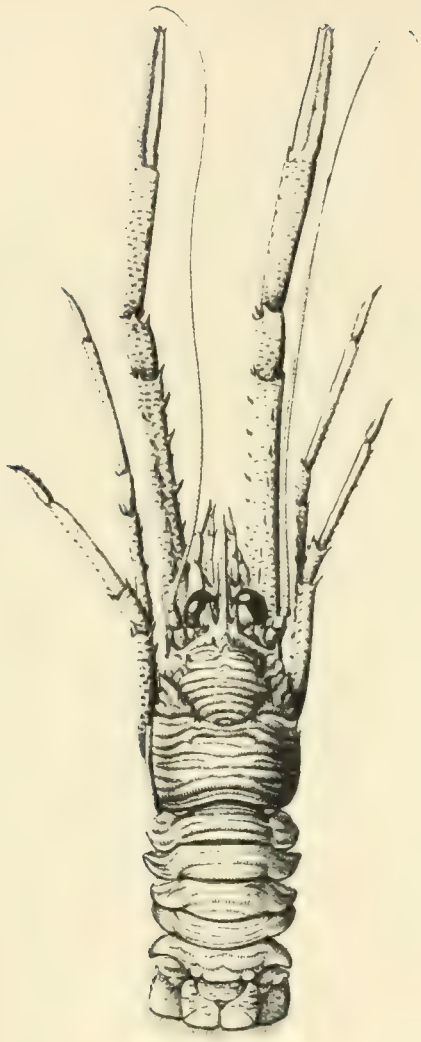

FIGURE 82.—*Munida irrasa* Milne Edwards. Animal in dorsal view (after Milne Edwards and Bouvier, 1897).

fingers agape at base; merus with rows of spines continued on carpus and hand. First pair of walking legs reaching proximal end of hand.

Abdomen without spines.

Measurements.—Length of carapace: males, 11 mm.; females, 14 mm.; smallest ovigerous female, 4 mm. (Chace, 1942).

Habitat.—Thirty to 260 fathoms.

Type locality.—Not designated with certainty.

Known range.—Off Cape Lookout, N.C.; Florida through West Indies to Grenada; Gulf of Mexico to Colombia and Venezuela; "600 mi. off St. Davids, Bermuda."

Remarks.—Ovigerous females have been taken off southeast Florida in July, and off North Carolina in September. The rhizocephalans *Cyphosaccus chacei* and *Boschmaia munidicola* were reported from *M. irrasa* by Reinhard (1958).

Family **Porcellanidae**

General form crablike. Carapace well calcified, depressed, regions usually not well defined; front often prominent but never with rostrum greatly projecting beyond eyes. Antennae inserted external to eyes, with three movable articles and a flagellum. Basal articles of antennules broad. Outer maxillipeds too large to be contained in buccal cavity. Chelipeds moderately elongate, usually broad and depressed. First, second, and third walking legs well developed; last leg feeble, reduced in size, inflexed and resting on carapace. Abdomen broad, symmetrical, composed of seven segments, bent under and held closely against thorax; males with a pair of pleopods on segment two, sometimes rudimentary or absent, females with a pair of pleopods on segments three, four, and five, those on three sometimes reduced or absent. Telson composed of five or seven well-calcified pieces (Haig, 1960).

KEY TO GENERA AND SPECIES IN THE CAROLINA

(Modified after Chace, 1942)

a. Form elongate, "hippalike"; telson much longer than broad ..... *Euceramus praelongus* (p. 109).

aa. Form less elongate; telson usually broader than long, never much longer than broad.

b. Lateral wall of carapace broken up into two or more pieces, separated by membranous interspaces; front triangular or transverse in dorsal view, never with projecting teeth; carapace subquadrate.

c. Carapace with numerous transverse tufts of setae; chelipeds and legs hairy ..... *Pachycheles pilosus* (p. 108).

cc. Carapace relatively smooth, not hairy; chelipeds deeply ridged and eroded, not hairy ..... *Pachycheles rugimanus* (p. 108).

bb. Lateral wall of carapace nearly always entire; if not, front distinctly tridentate in dorsal view; carapace not subquadrate.

c. Basal antennal article small, not joining margin of carapace, so that movable articles have free access to orbit ..... *Petrolisthes galathinus* (p. 107).

cc. Basal antennal article strongly produced forward and broadly in contact with margin of carapace, movable portion far removed from orbit.

d. Dactyls of walking legs armed with from two to four strong, fixed spines; carapace distinctly broader than long ..... *Polyonyx gibbesi* (p. 113).

dd. Dactyls of walking legs ending in a simple spine usually with small, movable accessory spinules on lower margin; carapace longer than broad.

e. Front strongly tridentate in dorsal view; carapace slightly longer than broad; chelipeds not grossly sculptured.

f. Cervical groove terminating anterolaterally in shallow marginal indentation at edge of carapace_____*Porcellana sayana* (p. 110).

ff. Cervical groove terminating anterolaterally in a distinct longitudinal cleft at edge of carapace____*Porcellana sigsbeiana* (p. 111).

ee. Front strongly trilobate in frontal view; carapace usually broader than long; chelipeds thick and grossly sculptured
Megalobrachium soriatum (p. 112).

Genus ***Petrolisthes*** Stimpson, 1858

Stimpson, 1858, p. 240.—Haig, 1960, p. 21.

Petrolisthes galathinus (Bosc)

Figure 83

Porcellana galathina Bosc, 1801 (or 1802), p. 233, pl. 6, fig. 2.
Petrolisthes galathinus: Hay and Shore, 1918, p. 404, pl. 29, fig. 1.—Haig, 1956, p. 22 (rev.).—1960, p. 36.

FIGURE 83.—*Petrolisthes galathinus* (Bosc). Animal in dorsal view, fifth leg only of left side shown, 5 mm. indicated.

Recognition characters.—Carapace a little longer than wide, covered with strong, transverse, ciliated rugae, scarcely interrupted at grooves separating well-marked regions; frontal region granulate, metabranchial regions plicate. Front produced into a broad, triangular, sinuous-sided rostrum with a broad median groove usually covered with short pubescence. Supraorbital spine present, not distinct in large specimens; postorbital angle produced into a small spine-tipped tooth; epibranchial spine strong. Eyes well developed. Antenna with first movable article bearing an anteromedian, spine-tipped, lamellar lobe; second and third articles lightly rugose.

Chelipeds large, covered with strong, ciliated rugae continuing obliquely and almost unbroken across carpus and hand, broken into series of shorter rugae on fingers; merus with a strong rugose lobe at inner distal angle; carpus about twice as long as wide, anterior margin with four to six strong serrate spines, a row of spines on posterior margin; hand broad, flattened, rugae on outer margin spiniform in smaller specimens, outer margin often fringed with plumose hairs; dactyl sinuous, fingers closing closely, a thick tuft of pubescence below. Walking legs rugose; anterior margin of meri with fringe of plumose hairs; all articles covered with long, nonplumose setae; anterior margin of first and second legs with six to nine spines, third with five to seven; merus of first and second with a posterodistal spine.

Sternum, sternal plastron, abdomen, ventral surface of outer maxillipeds, chelipeds, and walking legs covered with strong striations.

Measurements.—Length of carapace: males, 7 to 17 mm.; non-ovigerous females, 6 to 11 (15?) mm.; ovigerous females, 7 to 14 mm. (Haig, 1960; Holthuis, 1959).

Color.—Grayish brown without markings in life; in alcohol, light brown with purple or dark-red lines and dots on rugae (Hay and Shore, 1918). Spaces between rugae yellow; lower surface, including abdomen, deep red (Faxon *in* Haig, 1960).

Habitat.—Under stones and associated with sponges, corals, and anemones in littoral; in somewhat deeper water, from sand and sand-shell bottom (Haig, 1960); low-water mark to 27 fathoms.

Type locality.—Unknown.

Known range.—Cape Hatteras, N.C., through Gulf of Mexico and Caribbean area to Rio de Janeiro, Brazil; Ilha Trinidade off Brazil; Pacific Ocean from region around Panama City; Isla San Lucas, Costa Rica; off La Libertad, Ecuador.

Remarks.—A full review of this species has been given by Haig (1956, 1960). Ovigerous females are known from the Caribbean area from January to May, and from North Carolina and the Gulf of Mexico from June to September (Haig, 1956, 1960; Holthuis, 1959, in part).

Rathbun (1926) described a fossil species, *P. avitus*, from the Pliocene of Central America which is similar to the recent *P. galathinus*.

Genus ***Pachycheles*** Stimpson, 1858

Stimpson, 1858, p. 228.—Haig, 1960, p. 131 (rev.).

Pachycheles pilosus (H. Milne Edwards)

Figure 84

Porcellana pilosa H. Milne Edwards, 1837, p. 255.
Pachycheles pilosus: Haig, 1956, p. 11 (rev.).

Recognition characters.—Carapace slightly broader than long, flattened but somewhat more convex from front to back than side to side, lightly rugose along sides, with numerous short, transverse tufts of setae except scattered setae on frontal region. Frontal margin sinuous, slightly produced in middle, with a submarginal row of stout setae. Anterolateral margins emarginate. Epimeral pieces of metabranchial regions separated by membranous interspaces, posterior portion consisting of one or more pieces. Orbits deeply excavated, postorbital angle spiniform; eyes short, stout. Antenna with first movable article bearing a buttressed spine on anterior margin; second article with a spine near middle of anterior border; third article short, smooth.

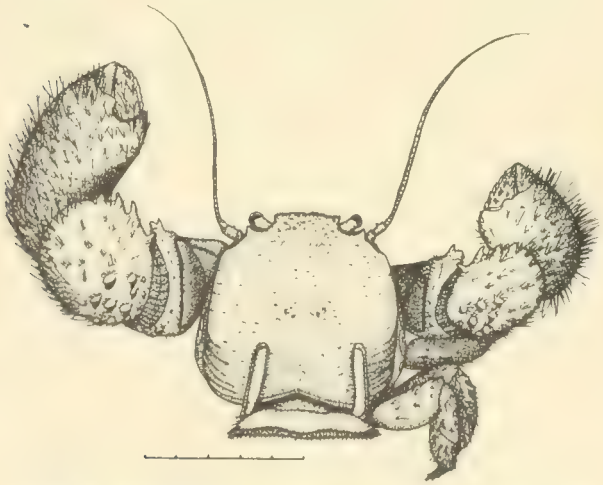

FIGURE 84. *Pachycheles pilosus* (Milne Edwards). Animal in dorsal view, second, third, and fourth leg of left side not shown. 5 mm. indicated.

Chelipeds unequal, stout, ornamented with numerous long, dark setae with shorter ones between; merus outlined dorsally with long setae, a stout spine and large white tubercle at inner distal angle; carpus with a number of prominent white tubercles on proximal portion, anterior border with about three spines; hand inflated, outer margin spined and tuberculate below and at base of immovable finger, fingers short, immovable finger with a single blunt tooth on cutting edge, inner edge of hand and dactyl with obsolescent spines. Walking legs with hairy covering similar to chelipeds, a few spines below on dactyls and propodi.

Telson of males and females with five elements.

Measurements.—Length of carapace: males, 7 mm.; ovigerous females, 5 to 7 mm. (Haig, 1956).

Habitat.—In corals; to 4 fathoms (Schmitt, 1935a).

Type locality.—Vicinity of Charleston, S.C.

Known range.—Charleston, S.C.; Key West to Sarasota Bay, Fla.; through West Indies to Tobago and Aruba.

Remarks.—Ovigerous females have been taken in the West Indies from February to May (Haig, 1956, in part). Rathbun (1926) reported a Pliocene species of *Pachycheles* from Central America.

Pachycheles rugimanus Milne Edwards

Figure 85

Pachycheles rugimanus Milne Edwards, 1880, p. 36.—Hay and Shore, 1918, p. 404, pl. 29, fig. 2.—Haig, 1956, p. 12 (rev.).

Recognition characters.—Carapace slightly longer than wide except in mature females, flat from side to side, convex from front to back, rugose along sides; anterolateral margins emarginate; epimeral pieces of metabranchial regions separated by membranous interspaces, posterior portion consisting of one or more pieces. Front broad, frontal margin projecting downward, slightly produced in middle, hardly visible from above. Orbits deeply excavated, margins slightly raised, postorbital angle spiniform; eyes short, stout, retractile. Antenna with first movable article bearing a serrate spine on anterior margin;

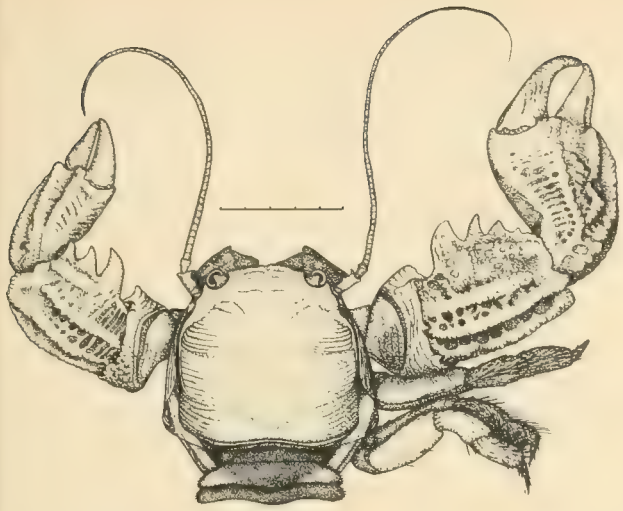

FIGURE 85.—*Pachycheles rugimanus* Milne Edwards. Animal in dorsal view, second, third, and fourth legs of left side not shown, 5 mm. indicated.

second article with a row of unequal spines on anterior border; third article short, smooth.

Chelipeds subequal, stout; merus crossed by a rew rugae distally, a rugose and serrate spine at inner distal angle; carpus with four anterior spines, graded in size, proximal one largest, and upper surface with four prominent longitudinal, tuberculate ridges, with deep channels between, channels crossed by irregular septae forming rows of oblong pits between ridges; ridges and pitted channels continued on hand but with less regularity in arrangement; fingers tuberculate almost to tips. First three pairs of walking legs stout and with distal articles hairy; last legs weak and reflexed dorsally.

Telson of male and female with five elements; male pleopods present.

Measurements.—Carapace: male, length, 8 mm.; width, 7 mm.; ovigerous female, length, 8 mm., width, 9 mm.

Color.—Brownish red, fingers vermilion.

Habitat.—To depth of 79 fathoms (Schmitt, 1935a).

Type locality.—Contoy, and west of Florida.

Known range.—Off Cape Lookout, N.C., through Florida to St. Thomas, V.I., and Contoy Island, Mexico.

Remarks.—Only a few collections of this species have been recorded, from widely scattered localities. Ovigerous females have been taken in February and March from the Carolinas and west Florida, and in September in North Carolina and east Florida.

Genus *Euceramus* Stimpson, 1860

Stimpson, 1860b, p. 445.—Haig, 1960b, p. 187.

Euceramus praelongus Stimpson

Figure 86

Euceramus praelongus Stimpson, 1860b, p. 444.—Hay and Shore, 1918, p. 405, pl. 29, fig. 3.—Haig, 1956, p. 7 (rev.).

Recognition characters.—Carapace subcylindrical, elongate; sides slightly arcuate, with minute, irregular, transverse rugae; anterolateral margins with two more or less obtuse spines on each side behind antennae. Front tridentate, median spine about twice length of lateral spines, a broad V-shaped depression at rear edge of carapace. Eyes well developed. Antennule short. Antenna about three-fourths length of body, flagella sparsely covered with fine hairs; basal article short, not produced forward; movable articles not far removed from orbit. Third maxilliped large, forming subquadrate shield extending laterally almost to edge of carapace.

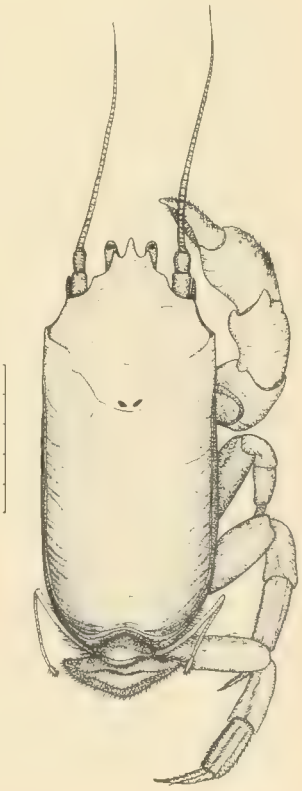

FIGURE 86.—*Euceramus praelongus* Stimpson. Animal in dorsal view, fifth leg only of left side shown, 5 mm. indicated.

Chelipeds stout, subequal; hand slightly roughened and hairy, somewhat stouter in males than in females; fingers about as long as palm, more gaping in males than in females. First pair of walking legs shorter than second and third pairs; last pair reduced and turned dorsally.

Abdomen small, distal segments narrow. Uropods reduced. Telson longer than broad, composed of seven elements.

Measurements.—Length of carapace from tip of rostrum to center of rear notch: males, 14 mm.; females, 14 mm.

Color.—Background of carapace greenish gray to greenish tan with lighter and darker lines of color delineating striae and marginal furrow; a light longitudinal stripe, broadest anteriorly, along middorsal line; purplish markings along lines separating major regions of carapace; legs mottled with greenish gray or tan as on carapace; a suggestion of iridescence on body and legs (from specimen collected by L. McCloskey, Morehead City Harbor, N.C., August 7, 1962).

Habitat.—Sandy beaches below waterline, and on broken-shell bottoms; low-water mark to 21 fathoms.

Type locality.—Beaufort, N.C.

Known range.—Chesapeake Bay, off South Marsh Island, to Aransas area of Texas coast.

Remarks.—Hay and Shore (1918) and Haig (1956) remarked that this is a rare species and it is true that it has seldom been collected, but the habits described by Pearse, Humm, and Wharton (1942) suggest that it is like a number of similar decapod crustaceans which are rare in collections chiefly because they live where they escape the attention of most collectors. Pearse, Humm, and Wharton described *E. praelongus* as a dweller of sandy beaches, similar in habit to *Emerita*, *Lepidopa*, and *Ogyrides*. It is also found on rubble-covered bottom. The animal is a highly adapted burrower which burrows backward. It scrapes food caught in the hairy antennae with setose mouth parts. Juvenile specimens are occasionally taken at night in plankton tows near inlets in North Carolina, and ovigerous females have been taken in May.

Haig (1960) placed *Euceramus* between the group of porcellanid "genera in which the basal antennal segment is short and not broadly in contact with the anterior margin of the carapace, and the group of genera in which the basal segment is strongly produced forward so that the movable segments are far removed from the orbit."

Genus *Porcellana* Lamarck, 1801

Lamarck, 1801, p. 153.—Haig, 1960, p. 196 (rev.).

Porcellana sayana (Leach)

Figure 87

Pisidia sayana Leach, 1820, p. 54.
Porcellana sayana: Hay and Shore, 1918, p. 403, pl. 29, fig. 7.—Haig, 1956, p. 31 (rev.).

Recognition characters.—Carapace usually a little longer than wide, depressed; dorsal surface slightly convex, meeting lateral parts in a slight shoulder a little behind base of antenna; surface minutely granulate and with fine oblique dorsal plications along sides, especially on posterolateral portions; a few scattered small clumps of hairs. Rostrum triangular, concave above, tip abruptly decurved, margins spinulate or tuberculate. Orbit with a strong tooth near inner angle, separated from orbit by a wide and rather deep notch; outer angle produced into a broad, low tooth. Eyes well developed. Cervical groove lightly impressed. Antennae slender, smooth, longer than carapace; basal article strongly produced forward into a spinelike projection; movable articles far removed from orbit.

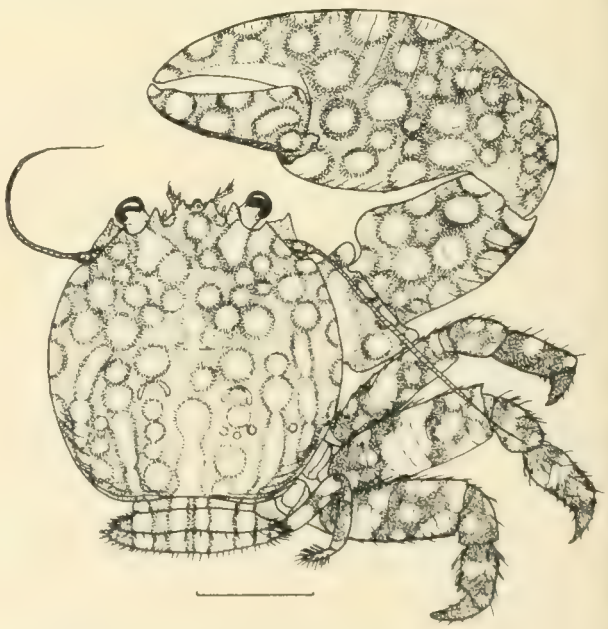

FIGURE 87.—*Porcellana sayana* (Leach). Animal in dorsal view, legs of left side not shown, 5 mm. indicated.

Chelipeds strong, heavy, finely plicate, nearly smooth in old individuals; hand as long as or longer than carapace, outer margin fringed with long hairs except in old individuals; fingers short, curved, and bent; proximal inner angle of carpus and distal inner angle of merus produced, forming lobes, both articles with scattered hairs near dorsolateral border, posterodistal angle of carpus ending in a spine. First three pairs of walking legs normal, with scattered hairs; last pair reduced and carried above others.

Telson composed of seven elements.

Measurements.—Carapace: males, length, 4 mm. (Wass, 1955), width, 12 mm.; nonovigerous females, length, 8 mm., width, 8 mm.; ovigerous females, length, 5 mm. (Haig, 1956) to 10 mm., width, 10 mm. Specimens with length and width equal are unusual.

Color.—Ground color reddish or rusty brown; covered on all dorsal surfaces and abdomen with complicated irregular pattern of yellowish white, yellow, and some bluish-white spots or longitudinal stripes; stripes more prominent on rear center part of carapace and on abdomen. Pattern quite variable in shape and shade, some specimens being predominantly light.

Habitat.—This species is often taken in the dredge in various parts of Beaufort Harbor, N.C., and along the neighboring coast. It has also been taken from among rocks of the jetties near Fort Macon. It is often found in crevices in clusters of oyster shells or as a commensal of the hermit crabs *Pagurus pollicaris* or *Petrochirus diogenes* in the shell of some gastropod. Hildebrand (1954) found specimens attached to the decorator crab, *Stenocionops furcata.* Shallow water to 48 fathoms; (390 fathoms(?), Schmitt, 1935a).

Type localities.—Coast of Georgia and Florida.

Known range.—Cape Hatteras, N.C., around Gulf of Mexico and Caribbean Sea to Bahia Caledonia, Panama; through West Indies to Venezuela and Surinam (Haig, 1956; Holthuis, 1959).

Remarks.—This species is rather abundant off the Carolinas and in the western Gulf of Mexico (Hildebrand, 1954, 1955). Ovigerous females are known to occur from January to November in various localities throughout the range. In North Carolina, they are known in January and from June to November. Brooks and Wilson (1883) described the first zoeal stage of *P. sayana.* A long breeding season is indicated, as is true of a close relative in the Pacific, *Porcellana cancrisocialis.* Haig (1960) suggested that these forms may be conspecific.

Porcellana sigsbeiana Milne Edwards

Figure 88

Porcellana sigsbeiana Milne Edwards, 1880, p. 35.—Benedict, 1901, p. 137.—Milne Edwards and Bouvier, 1923, p. 292, pl. 1, fig. 6.—Haig, 1956, p. 33 (rev.).

FIGURE 88.—*Porcellana sigsbeiana* Milne Edwards. Animal in dorsal view, fifth leg only of left side shown, 5 mm. indicated.

Recognition characters.—Carapace longer than wide, evenly convex in posterior half, broadly ridged in gastric region; lateral margins thin, produced, and slightly upturned; surface faintly rugose. Front strongly tridentate; rostrum exceeding narrower lateral teeth, irregularly pentagonal with sides adjacent to base subparallel. Orbit with outer angle produced into a broad, oblique tooth; eyes well developed. Anterolateral

borders concave, ending in a shoulder separated from acute marginal tooth by an elongate notch at terminus of cervical groove. Antennae slender, smooth, about as long as carapace; basal article strongly produced forward in a spinelike projection; movable articles far removed from orbit.

Chelipeds strong, heavy, smooth; hand longer than carapace, outer margin fringed with hairs; fingers less than half as long as palm, nearly straight, hooked at tips; length of carpus more than 1.5 times width, a single small spiniform tooth on anterior border; merus with a single broad tooth on lobe at internal angle. First three pairs of walking legs with scattered tufts of hairs; last pair reduced and carried above others.

Telson composed of seven elements.

Measurements.—Male carapace: length, 24 mm., width, 22 mm.

Color.—Colored with an irregular pattern of reddish longitudinal mottlings on a white background (specimens preserved in alcohol).

Habitat.—The species occurs near the edge of the Continental Shelf in North Carolina, and is usually found in deeper water than the related and similar species, *Porcellana sayana;* 27 to 215 fathoms.

Type localities.—Blake Stations: 49, off delta of Mississippi River, 118 fathoms; 36, north of Yucatan, 84 fathoms; 142, Flannegan Passage [V.I.], 27 fathoms.

Known range.—Off Marthas Vineyard, Mass., to northern Gulf of Mexico and southern Gulf of Mexico off Yucatan; West Indies to Virgin Islands.

Remarks.—Ovigerous females have been taken in April, May, June, and November off northwest Florida, Alabama, Mississippi, and Louisiana, and in midwinter off Yucatan. Benedict (1901) was correct in stating that this is the largest porcellanid species in the region.

Genus *Megalobrachium* Stimpson, 1858

Stimpson, 1858, p. 228.—Haig, 1960, p. 212.

Megalobrachium soriatum (Say)

Figure 89

Porcellana soriata Say, 1818, p. 456.—Hay and Shore, 1918, p. 404, pl. 29, fig. 6.
Porcellanopsis soriata: Haig, 1956, p. 35.
Megalobrachium soriatum: Haig, 1960, p. 227 (rev.).

Recognition characters.—Carapace somewhat hexagonal, slightly wider than long; margins more or less hairy; areolations well marked, some tuberculate. Front rounded in dorsal view, trilobate in frontal view; rostrum little, if any, longer than lateral teeth. Orbits well defined; eyes well developed. Antennae about as long as carapace; basal article strongly produced forward and broadly in contact with margin of carapace; movable articles slender and removed from orbit.

Chelipeds long and heavy, roughly tuberculate; hand fringed with long hair along lower margin and with tubercles in rather well-defined rows; fingers with white, strongly hooked tips; carpus with one strong spine and some smaller spines on anterior border, dorsal aspect with tubercles irregularly arranged and appearing granulate under slight magnification; merus ornamented like carpus distally. First three walking legs stout, hairy, and with sharp, curved dactyls; last legs weak and placed above others.

Telson divided into five elements.

Measurements.—Carapace: length of male, 5 mm., width, 5.5 mm.; ovigerous females, length, 4 to 5 mm., width, 4 to 5.5 mm.

Color.—In life a dirty gray; in alcohol a rusty or grayish red.

Habitat.—Free living among corals, rocks, and sponges; in North Carolina found especially in canals of sponges taken from fishing banks offshore near Beaufort Inlet (Hay and Shore, 1918;

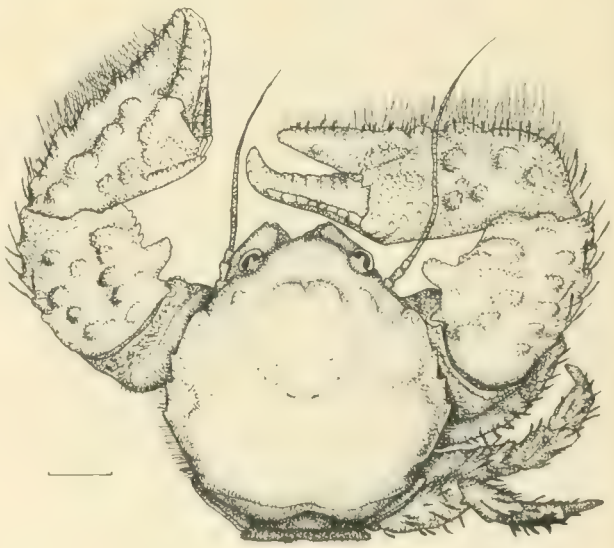

FIGURE 89.—*Megalobrachium soriatum* (Say). Animal in dorsal view, second, third, and fourth legs of left side not shown, 1 mm. indicated.

Pearse and Williams, 1951). Wass (1955) found the species in sponges of the genus *Ircinia* in Florida. Near low-water mark to 37 fathoms.

Type locality.—St. Catherines Island, Ga.

Known range.—Off Cape Hatteras, N.C., to Port Aransas, Tex.; West Indies to Barbados; Contoy, Mexico; Bahia Caledonia, Panama.

Remarks.—This small porcellanid crab has had a varied taxonomic history. First, Say's trivial name was misspelled by subsequent authors (*sociata* for *soriata*), as pointed out by Benedict (1901), and second, the generic designation has been changed four times as understanding of relationships has been variously interpreted. Chace (1942) shifted *soriata* from *Porcellana* to *Porcellanopsis*. The most recent reviser (Haig, 1960), after reviewing all species referred to *Megalobrachium* and *Porcellanopsis*, deemed it best to combine all forms in a single genus.

A close congener of the eastern Pacific is *M. tuberculipes* (Lockington), and Haig suggested that they may not be distinct.

Ovigerous females have been taken off the Carolinas in June, July, and August, and in July in Florida (Wass, 1955).

Genus ***Polyonyx*** Stimpson, 1858

Stimpson, 1858, p. 233.—Haig, 1960, p. 232.

Polyonyx gibbesi Haig

Figure 90

Porcellana macrocheles Gibbes, 1850, p. 191.

Polyonyx macrocheles: Hay and Shore, 1918, p. 405, pl. 29, fig. 8.

Polyonyx gibbesi: Haig, 1956, p. 28 (rev.).

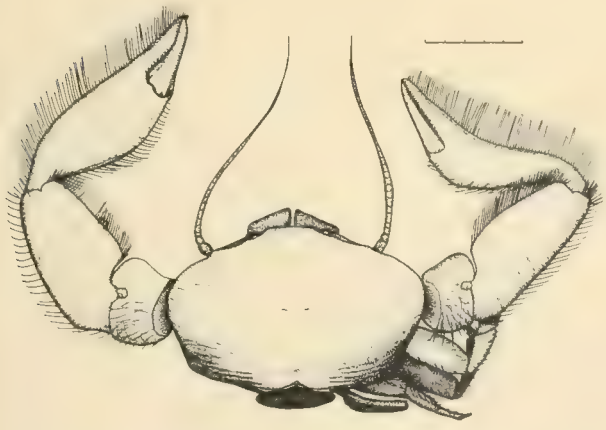

FIGURE 90.—*Polyonyx gibbesi* Haig. Female in dorsal view, second, third, fourth, and fifth legs of left side not shown, 5 mm. indicated.

Recognition characters.—Carapace smooth, finely plicate, transversely oval, about one-fourth to one-third wider than long; front hardly produced, margin slightly sinuous; posterolateral portions with scattered, feathered hairs; infolded lateral portions separated from rest of carapace by a deep fissure. Orbits small, eyes small, cornea reduced. Antenna slender, about 1.5 times as long as body; basal article strongly produced forward; movable articles far removed from orbit.

Chelipeds unequal, long and distorted; larger hand nearly twice as long as carapace; superior margin of hands convex, with thin fringe of plumose hairs, inferior margin nearly straight, with fringe of long plumose hairs; distal two-thirds of propodus with single row of fine, close-set, subtruncate teeth, larger and less closely set distally (row longer on small hand); fingers short, hooked at tip, toothed on cutting edges, dactyl falciform, sparsely hairy (straighter on small hand); carpus as long as palm, thick, anterior margin produced into a thin crest, proximal end markedly subrectangular, entire margin with fringe of fine plumose hairs, a thinner fringe of shorter hairs on outer margin; merus subcubical, finely rugose above, upper margin produced in front, plumose-hairy dorsolaterally. First three pairs of walking legs sparsely hairy, last pair with long tuft on chela and distal end of carpus; merus of second and third legs spinulose below, dactyls of first to third legs with four corneous spines on internal margin closing against weaker spines on distal portion of propodus.

Measurements.—Carapace: male, width, 11 mm.; nonovigerous female, length, 9 mm., width, 13 mm.; ovigerous female, width, 16 mm.

Color.—Grayish white, sometimes stained with brown.

Habitat.—A common commensal of the annelid *Chaetopterus variopedatus* [=*pergamentaceus*], seldom found outside tubes of this worm; intertidal to 8 fathoms.

Type locality.—Coast of South Carolina.

Known range.—Woods Hole, Mass.; Rhode Island; Beaufort, N.C., to Alligator Harbor, Fla.; Puerto Rico; Bahia Caledonia, Panama. Notes in Haig's (1956) account for *P. gibbesi* indicate that the species may range to Brazil.

Remarks.—It is unfortunate that this distinctive species, known so long under the name *Poly-*

onyx macrocheles (Gibbes), should have to undergo a name change, but Haig (1956) has shown that *Porcellana macrocheles* Gibbes, 1850, is a homonym of *Porcellana macrocheles* Poeppig, 1836, hence unavailable. The substitute name is quite appropriate, however, for it not only honors the original describer but is applied to a species common in the area where he worked.

Unlike other porcellanids occurring in the Carolinas, *Polyonyx gibbesi* has been the subject of some ecological observations. Enders (1905), at Beaufort, N.C., and Pearse (1913), at Woods Hole, Mass., studied commensal inhabitants of the tubes of *Chaetopterus variopedatus*, finding *P. gibbesi* to be common commensals in both areas. Both authors found usually a male and a female crab in the same tube, but Enders found six isolated ovigerous females in the course of a summer. Pearse found the species to be strongly thigmotactic, and crabs, seemingly too large to enter *Chaetopterus* tubes, entered and left an artificial tube at will in the laboratory.

Individuals usually moved backward or sideways on open sand, using the chelipeds as an aid in walking, or at times swam clumsily upside down by flapping the abdomen. Individuals showed little ability to burrow. The respiratory mechanism seemed well adapted to life in confinement, for the respiratory currents were strong and capable of being directed, changing with the change in direction of waterflow in the worm tube. Crabs in an experimental tube tolerated considerable fouling of the water.

Pearse gave an excellent figure of the detailed structure of the chelate and tufted fourth walking legs which are used extensively in the meticulous preening characteristic of this species. The plumes of hairs on the appendages, especially those on the third maxillipeds, are used as nets for capturing food from water currents.

Gray (1961) reviewed the life history and ecology of the species. He found that the breeding season at Beaufort, N.C., extends at least from April to December, and ovigerous females are otherwise known in February and March from Florida. Usually when a pair of *P. gibbesi* is found in a tube, adult crabs of no other species are present at the same time. The smallest female with eggs was 8.4 mm. in width. Gray concluded that the crabs enter worm tubes by chance, not in response to attractants.

In the years since Enders' and Pearse's studies, the proportion of *Pinnixa chaetopterana* to *Polyonyx gibbesi* at Woods Hole and Beaufort has changed. Woods Hole; *Polyonyx-Pinnixa;* 1913, 22:78; 1959, 66:34. Beaufort; 1905, 83:17; 1958–59, 39: 61. Gray (1961) postulated that the more southerly species, *P. gibbesi*, has increased in the Woods Hole area due to amelioration of climate. In the Beaufort area, decline may be due to recent hurricane damage which destroyed many *Chaetopterus* tubes. Gray also found that *P. gibbesi* prefers less muddy bottoms than *P. chaetopterana.* He considered *P. gibbesi* an obligate commensal of *Chaetopterus.*

Faxon (1879) discussed the last stage zoea of *P. gibbesi* and determined that it molts directly into the first crab stage with no intervening megalops as in brachyurans. Smith (1880b) reported swarms of zoeae of *P. gibbesi* at the edge of tidal currents near the mouth of Narragansett Bay in summer.

Superfamily **Paguridea**

Carapace elongate and subcylindrical, or broad and crablike; front not fused with epistome. Abdomen soft, asymmetrical, and spirally coiled, merely bent or flexed against thoracic sterna as in Brachyura, or rarely symmetrical, straight and well calcified dorsally. Tail fan usually present and asymmetrical, occasionally symmetrical. Eyes never in orbits. Antennal peduncle five jointed; second article almost always with a movable acicle. First pair of legs chelate and usually large; fifth pair always, and fourth pair commonly, much less developed than preceding pairs. Abdominal appendages usually unpaired on second to fourth, or second to fifth segments, and usually present only on left side (Alcock, 1905).

Family **Paguridae.** Hermit crabs

Carapace usually somewhat elongate and broadened posteriorly, sides membranous, and covered with a network of very thin lines ordinarily limited above by *linea anomurica.* Abdomen generally soft and spirally coiled in adaptation to gastropod shells (abdomen secondarily symmetrical in a few forms using other kinds of

housing). Eye scales triangular. Thoracic sternites, corresponding to third, fourth, and fifth legs, free and mobile. Legs four and five reduced and modified. Middle terga of abdomen separated more or less by membrane (adapted from Alcock, 1905; Bouvier, 1940).

Remarks.—A most useful bibliography of this group was published by Gordan (1956). The family Paguridae has a long fossil record in North America. Species of *Paguristes*, *Petrochirus*, and *Pagurus* are known from the Cretaceous, and *Dardanus* from the Eocene (Rathbun, 1935).

KEY TO SUBFAMILIES IN THE CAROLINAS

a. Third maxillipeds approximated at base; chelipeds subequal, or left much larger than right, rarely with right slightly larger than left____Diogeninae (p. 115).
aa. Third maxillipeds widely separated at base by a sternum; right cheliped usually much larger than left, left never larger than right, occasionally subequal
Pagurinae (p. 125).

Subfamily **Diogeninae**

The chief distinguishing characters are given in the above key.

KEY TO GENERA AND SOME SPECIES OF DIOGENINAE IN THE CAROLINAS

a. Paired appendages present on first two abdominal segments of male, and first abdominal segment of female; fingers of chelipeds opening and closing horizontally
Paguristes (p. 115).
aa. No paired appendages on anterior abdominal segments in either sex.
b. Fingers of chelipeds opening and closing horizontally_____*Clibanarius vittatus* (p. 120).
bb. Fingers of chelipeds opening and closing obliquely or nearly vertically.
c. Chelipeds not markedly unequal, right usually slightly larger than left
Petrochirus diogenes (p. 122).
cc. Chelipeds markedly unequal, left much larger than right_____*Dardanus* (p. 123).

Genus ***Paguristes*** Dana, 1852

Provenzano, 1959, p. 381 (rev.).

KEY TO SPECIES IN THE CAROLINAS

a. Rostrum broadly rounded, or pointed, but not advanced beyond level of lateral projections on front.
b. Anterolateral sides of anterior shield of carapace not spiny_____*moorei* (p. 115).
bb. Anterolateral sides of anterior shield of carapace definitely spiny_____*lymani* (p. 116).
aa. Rostrum slender, and definitely advanced beyond level of lateral projections on front.
b. Anterior shield of carapace not noticeably longer than broad.
c. Frontal and lateral margins meeting at almost a right angle_____*sericeus* (p. 117).
cc. Frontal and lateral margins meeting at broadly obtuse or rounded angle_____*triangulatus* (p. 118).
bb. Anterior shield of carapace noticeably longer than broad.
c. Eye scales acuminate_____*spinipes* (p. 118).
cc. Eye scales with three or four (occasionally two) terminal spines_____*tortugae* (p. 119).

Paguristes moorei Benedict

Figure 91

Paguristes moorei Benedict, 1901, p. 144, pl. 4, fig. 3.—Hay and Shore, 1918, p. 409, pl. 30, fig. 3.

Recognition characters.—(Taken from holotypic female.) Anterior shield of carapace slightly longer than broad; upper surface of carapace with a few scattered hairs and irregular punctations, more or less iridescent. Rostrum short, obtusely pointed, slightly less advanced than more acute lateral projections. Eyestalks slender, slightly dilated distally, slightly longer

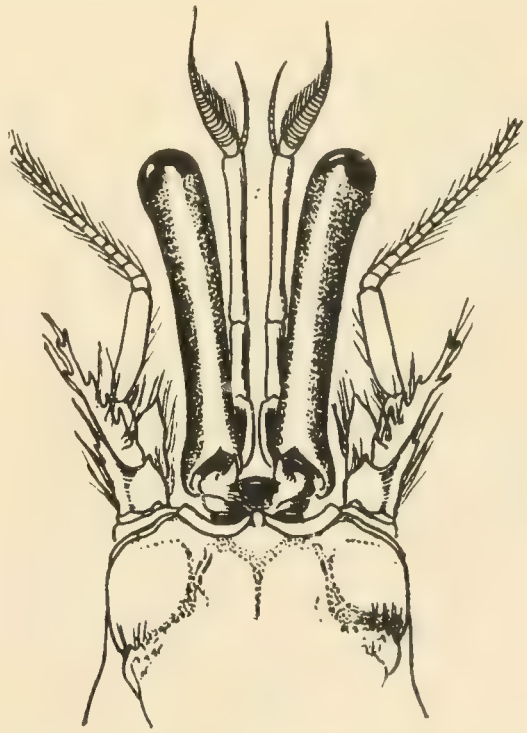

FIGURE 91.—*Paguristes moorei* Benedict. Type female, anterior part of body in dorsal view, approximately × 5 (after Benedict, 1901).

than width of anterior shield (8.6 mm.); eye scales not adjacent, anterior process acute. Antennular peduncle slightly exceeding eyestalk when extended. Antennal peduncle extending slightly beyond middle of eyestalk; flagellum not exceeding tips of legs, with scattered setae; acicles bispinose at tip (right spine on right acicle broken), a row of four strong spines on proximal two-thirds of inner side (right acicle with a single external spine).

Chelipeds subequal but of similar form, medial margins nearly straight; hands short and thick, covered dorsally with many tubercles and hairs, but nearly smooth ventrally, a row of strong spines on upper medial border of palm, edges of fingers fitting closely; carpus similar to hands but with fewer tubercles in two rows, largest tubercles on medial upper border; merus prismatic with tubercles on angles. First pair of walking legs with a row of spines along upper margin of carpus and propodus.

Measurements.—Carapace (holotypic female): length in midline, 13.2 mm., width, 11.8 mm.; anterior shield, length, 8.5 mm., width, 8.3 mm.

Color.—Yellowish, eyestalks deep orange or crimson below, and white above (Hay and Shore, 1918).

Habitat.—From near edge of continental shelf in North Carolina.

Type locality.—Puerto Rico.

Known range.—Gulf Stream about 30 miles south of Cape Lookout, N.C.; Puerto Rico.

Remarks.—The species is known from only two specimens. The type only is extant.

Paguristes lymani Milne Edwards and Bouvier

Figure 92

Paguristes lymani Milne Edwards and Bouvier, 1893, p. 49, pl. 4, figs. 13–22.—Benedict, 1901, p. 145, pl. 4, fig. 8.—Alcock, 1905, p. 157.

Recognition characters.—Anterior shield of carapace slightly broader than long, sides a little hairy and roughened by spiny granules; posterolateral corners notched. Rostrum often a rounded lobe falling far short of pointed lateral projections; front rounding gradually to lateral margins from lateral projections. Eyestalks somewhat dilated at base and longer than distance between apices of lateral projections of front; eye scales singly acuminate or with up to three unequal spines on anterior border, long hairs somewhat obscuring tip. Antennular peduncles highly variable, exceeding eyestalks from less than half to entire length of terminal article. Tips of antennal peduncles extending to base of cornea, or slightly beyond eyes; acicles extending to three-fourths length of eyestalks, terminated by a spiny fork and often with three to five spinules on internal or external borders, external spine at base of acicle also spinulose on outer margin.

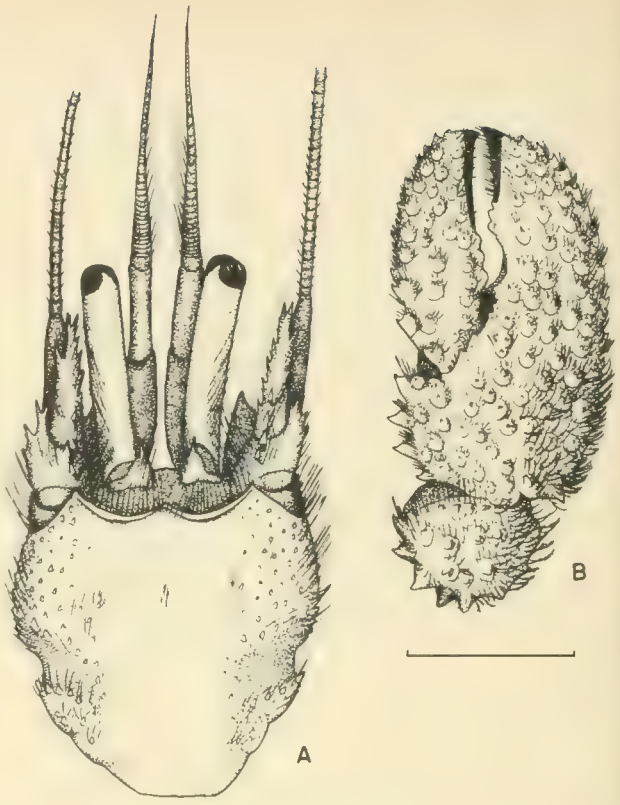

FIGURE 92.—*Paguristes lymani* Milne Edwards and Bouvier. A, anterior part of body in dorsal view; B, right chela, outer surface; 5 mm. indicated.

Chelipeds small, subequal, and similar; hands about twice as long as broad, upper surface covered with rather large tubercular granules, many with corneous tips, and four spines on internal margin of palm; lower margin of palm concave at base of immovable finger; fingers slightly agape, terminated by corneous tips preceded by finely denticulate cutting edges, dactyl with four or five small teeth behind corneous portion; carpus with three rows of spines on upper surface, four or five large ones on inner margin, about six on outer margin (with distalmost largest), and

about six more on upper surface near inner margin; superior border of merus armed with more or less pointed projections, feebly rugose externally; spines of palm, carpus, and merus obscured by feathered hairs. Walking legs with long hairs, particularly on upper and lower borders of dactyls; spines on crest of carpus, propodus, and base of dactyl, and somewhat reduced ones on inner and outer sides of propodus and carpus where rows appear mixed with hairs; dactyls arched, somewhat shorter than combined length of two preceding articles, and terminated by a conical claw.

Measurements.—Length of carapace: males, 13 mm.; ovigerous females, 11 mm.

Variations.—The spination of the chelipeds may vary in strength and density. The length of the antennular peduncles, in relation to the eyestalks, is highly variable. The eye scales become more dentate with age [implied]. The rostrum may reach the level of the lateral projections of the front, and small individuals tend to be hairier than large ones (Milne Edwards and Bouvier, 1893).

Habitat.—Literature and museum records show that this species has been found housed in small to medium-sized shells belonging to the families Cassididae, Dentaliidae, Nassariidae, Ovulidae, Muricidae, Trochidae, Turridae, and Volutidae; 15 to 878 fathoms.

Type locality.—Sand-Key, [Fla.], 15 fathoms.

Known range.—Southeast of Cape Lookout, N.C. (82–100 fathoms); Florida Keys to Swan Island off Honduras; through West Indies to British Guiana.

Remarks.—Ovigerous females have been taken in February from North Carolina and Florida, in May and June from Florida, and in November from British Guiana.

Paguristes sericeus Milne Edwards

Figure 93

Paguristes sericeus Milne Edwards, 1880, p. 44.—Milne Edwards and Bouvier, 1893, p. 46, pl. 3, figs. 14–22.—Provenzano, 1961, p. 155.

Paguristes rectifrons Benedict, 1901, p. 145, pl. 4, fig. 7.

Recognition characters.—Anterior shield of carapace nearly as broad as long, flattened, with several spines on each side; frontal margin as long as ocular peduncles, making nearly a right angle with lateral margins; lateral projections

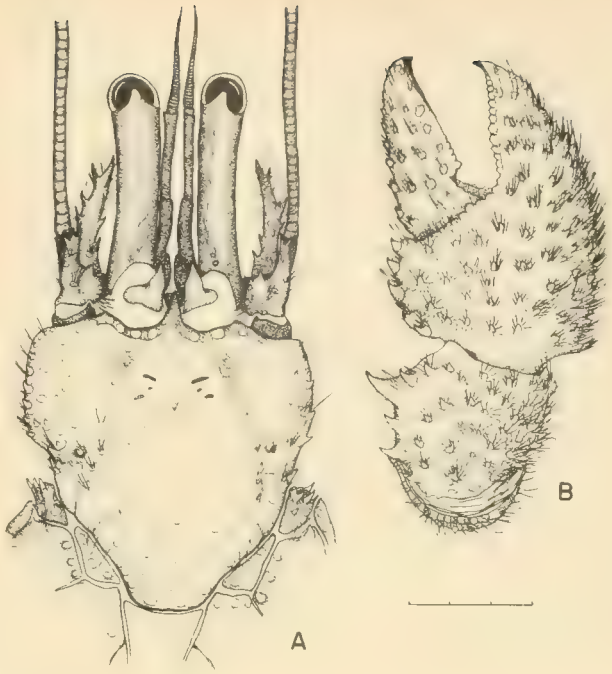

FIGURE 93.—*Paguristes sericeus* Milne Edwards. A, anterior part of body in dorsal view; B, right chela, outer surface; 3 mm. indicated.

low but terminating in a small spine. Rostrum with acute tip reaching along approximately half length of eye scales. Ocular peduncles slightly narrowed in middle; eye scales small, acuminate at tip. Antennular peduncles extending almost to tips of eyestalks. Antennal peduncles slightly exceeding acicles, terminal article armed with two spines; acicles straight, terminated by a spiny fork and with two or three spines on internal and external borders.

Chelipeds subequal, and rather short and broad; upper surface of hands and carpi with soft, silky, yellow hairs nearly obscuring surface, many strong granulations becoming corneous at tips scattered over upper surface. Walking legs not reaching much beyond extended chelipeds; dactyls regularly curved, dactyl of first walking leg 1.5 times length of propodus, of second as long as propodus and carpus combined.

Measurements.—Length of carapace: approximately 20 mm. (Milne Edwards and Bouvier, 1893).

Variations.—There is apparently some variation in straightness of the front and length of the eyestalks, as judged by the accounts of Milne

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Edwards and Bouvier (1893) and Benedict (1901).

Color.—Body reddish with white spotting; eyestalks not spotted but solid orange red (from recently preserved specimen and from Provenzano, 1959, 1961).

Habitat.—Coral rubble and sand; found in *Strombus*, *Murex*, and *Oliva* (Provenzano, 1961, and various authors); 5 to 36 fathoms.

Type locality.—Lat. 24°34′ N. long. 83°16′ W. [near Dry Tortugas, Fla.], 36 fathoms.

Known range.—Off Cape Lookout, N.C.; Florida Keys to Virgin Islands.

Remarks.—Ovigerous females are known from the Virgin Islands in April (Provenzano, 1961).

Paguristes triangulatus Milne Edwards and Bouvier

Figure 94

Paguristes triangulatus Milne Edwards and Bouvier, 1893, p. 40, pl. 4, figs. 6–12.—Benedict, 1901, p. 146, pl. 4, fig. 9.—Alcock 1905, p. 157.

Recognition characters.—Carapace somewhat hairy toward sides, and with scattered hairs on anterior shield; shield a little longer than broad; front with a thickened margin and a pointed rostrum reaching well beyond broadly angular lateral projections. Eyestalks long, slightly dilated, but obliquely compressed at tips, a line of hairs along dorsal side; eye scales acuminate, a little rugose on internal border. Antennular peduncles with about half of terminal article extending beyond eyestalks. Antennal peduncles extending to base of cornea or as little as three-fourths length of eyestalks; acicles reaching about to middle of eyestalks, spinose on internal and external borders, tip often bifurcate.

Chelipeds subequal, similar, upper surfaces tuberculate and hairy; inner margin of hands, carpi, and bases of dactyls with strong spines corneous at tips; upper surfaces of carpi and meri with a few spines and spiniform tubercles corneous at tips. First walking legs with spiny crest on carpi, propodi, and base of dactyls, crest obsolescent on second pair, both pairs hairy dorsally; dactyls curved, about as long as two preceding articles together; dactyls of right side a little weaker than left and laterally compressed; proximal end of first left dactyl with cross section in form of curvilinear triangle, broadly rounded internal face serving as base and obtusely pointed external face serving as apex; second left dactyl a little stronger.

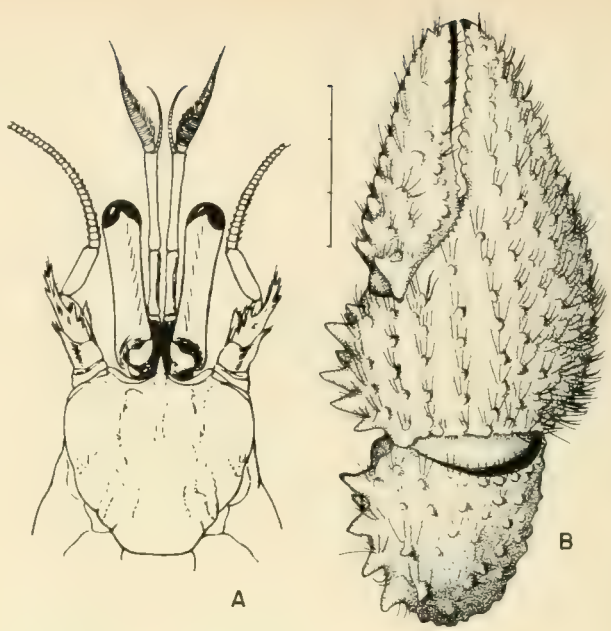

FIGURE 94.—*Paguristes triangulatus* Milne Edwards and Bouvier. A, anterior part of body in dorsal view, approximately × 3 (after Benedict, 1901); B, right chela, outer surface, 3 mm. indicated.

Measurements.—Length of carapace: male, 11 mm.; ovigerous female, 12 mm.

Color.—Legs and anterior part of cephalothorax tinted pink (Milne Edwards and Bouvier, 1893); eyestalks pink (Benedict, 1901).

Habitat.—One specimen has been reported from a shell of *Murex* (Milne Edwards and Bouvier, 1893); 6.5 to 82 fathoms.

Type locality.—Barbados, 73 fathoms.

Known range.—Off Oregon Inlet, N.C. (6.5 fathoms); Tortugas, Fla.; Barbados; Trindad.

Remarks.—Ovigerous females have been taken from Florida in August and October.

Paguristes spinipes Milne Edwards

Figure 95

Paguristes spinipes Milne Edwards, 1880, p. 44.—Milne Edwards and Bouvier, 1893, p. 33, pl. 3, figs. 1–13.—Benedict, 1901, p. 145, pl. 4, fig. 6.—Alcock, 1905, p. 157.—Boone, 1927, p. 76.
Paguristes visor Henderson, 1888, p. 78, pl. 8, fig. 3.
Paguristes armatus Hay, 1917, p. 73.—Hay and Shore, 1918, p. 409, pl. 30, fig. 7.

Recognition characters.—Anterior shield of carapace convex, considerably longer than broad; frontal margin thickened and drawn out into an almost straight-sided, acute rostrum, with tip con-

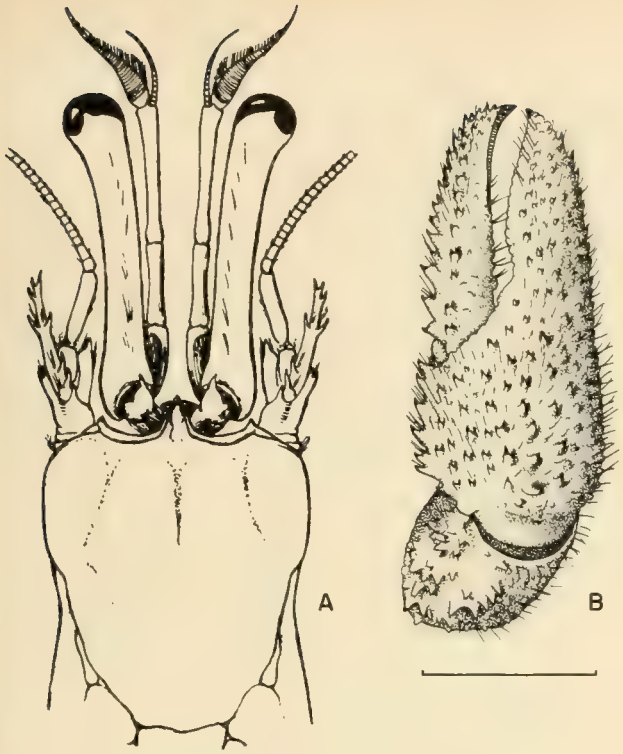

FIGURE 95.—*Paguristes spinipes* Milne Edwards. A, anterior part of body in dorsal view, approximately × 4 (after Benedict, 1901); B, right chela, outer surface, 5 mm. indicated.

siderably exceeding rather obtuse lateral projections. Eyestalks considerably longer than greatest width of front but not quite so long as length of anterior shield, somewhat contracted in middle and slightly bent laterally, not much dilated distally; eye scales acuminate. Antennular peduncles extending to tips of, or a little beyond, eyestalks. Antennal peduncles extending about two-thirds length of eyestalks; acicles straight, terminated by a spiny fork, and with two or three spines on internal and external borders.

Chelipeds subequal and similar in form, narrow but massive; hands less than half as broad as long; upper surface of hands and carpi covered with conical spines, many with corneous tips, strongest on superointernal border; fingers more than half as long as whole of propodus and terminating in corneous tips, opposed edges with numerous teeth. Walking legs extending a little beyond chelipeds, ornamented with tufts of hair most numerous and rigid on dactyls; dactyls regularly curved and half again as long as propodus; crest of spines on carpus and propodus extending along a portion of dactyl of first walking legs, but reduced, and present on carpus only of second walking legs.

Measurements.—Length of carapace: adults, 17 mm.; immatures, approximately 5 mm. (Milne Edwards and Bouvier, 1893, in part).

Variations.—The eyestalks are somewhat shorter than the front in young individuals but much longer in adults; they are frequently unequal in length. The cardiac region is calcified but the areas lateral to it are variably calcified (Milne Edwards and Bouvier, 1893).

Color.—A spot of orange red on external and internal faces of first walking legs, less definite on two following pairs; occasionally, traces of red coloration on anterior part of cephalothorax (Milne Edwards and Bouvier, 1893). In alcohol, nearly white, each cheliped with a conspicuous orange-yellow band across merus and a faint trace of a similar band on each walking leg (Hay and Shore, 1918).

Habitat.—This essentially deep-water hermit has been taken from shells of *Cassis* and *Xenophora;* 73 to 350 fathoms.

Type locality.—Grenada, 92 fathoms.

Known range.—Gulf Stream south of Cape Lookout, N.C., off Cape Canaveral and Sarasota, Fla.; Barbados to Pernambuco, Brazil.

Remarks.—This species has rarely been collected north of Barbados.

Paguristes tortugae Schmitt

Figure 96

Paguristes tortugae Schmitt, 1933, p. 7, fig. 4.—Provenzano, 1959, p. 388, fig. 11 (rev.).

Recognition characters.—Anterior shield of carapace longer than broad; rostrum triangular, in advance of lateral projections of front. Eyestalks slender, straight, as long as greatest width of anterior shield; eye scales separated by rostrum, anterior process armed with three or four spines (occasionally two) decreasing in size from median spine outward. Antennular peduncles reaching to base of cornea or slightly beyond. Antennal peduncles reaching to three-fourths length of eyestalks; flagella not reaching to tips of chelipeds, sparsely setose; acicles obscured by hairs, armed with two spines on inner edge and at least three on outer edge.

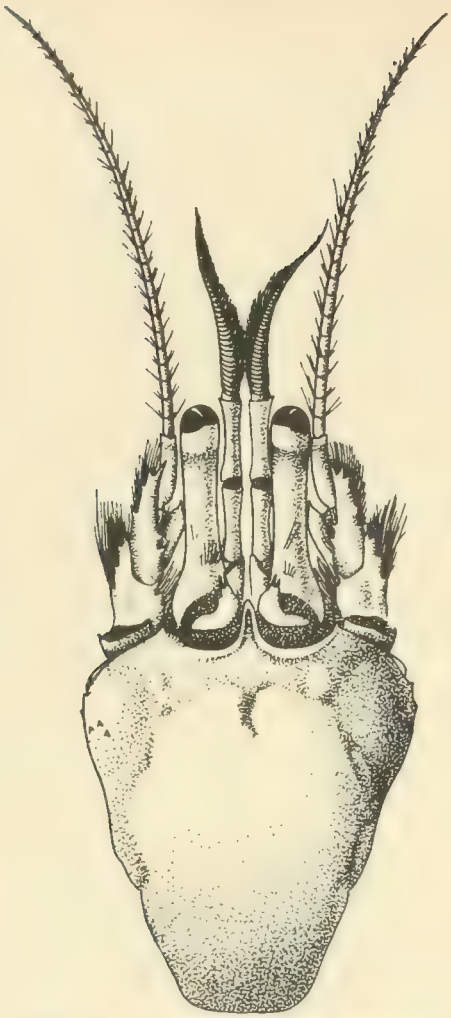

FIGURE 96.—*Paguristes tortugae* Schmitt. Anterior part of body in dorsal view, × 10 (after Holthuis, 1959).

Chelipeds equal, thickly covered with hairs, medial margins of chelae and carpi straight, fitting closely together when retracted; hands with forwardly directed, hooked spines on median upper surface, inner margin, outer half, and outer margin of immovable finger, hairs arising along anterior part of base of tubercles giving a squamose appearance; dactyl with seven more or less distinct, transverse rows of small, horny-tipped tubercles, largest on upper margin; fingers with tips corneous, more or less spooned; lower surface of chela smooth except for some tufts of hairs. First and second walking legs with heavy fringes of hairs along upper and lower margins and some tufts on lateral surfaces, outer surface smooth; dactyls somewhat longer than propodi, tips dark, corneous, a row of similar colored spinules on ventral border; inner surface of dactyls and propodi with squamiform tubercles near upper and lower margins, more pronounced where bases of hairs coincide with squamous tubercles. First walking legs with upper surface of propodus serrate, and a few denticles at base of dactyl. Second legs with two rows of spines on carpus, one on upper margin and one on upper portion of inner surface, a shallow groove on upper part of inner surface extending distad from carpus. Third legs with a single row of spines on carpus; merus of second and third legs with an anteroventral spine.

Measurements.—Length of carapace: male, 10 mm.; ovigerous female, 7 mm. (Provenzano, 1959).

Variations.—Holthuis (1959) described a somewhat longer rostrum, a longer antennular peduncle, a somewhat spinier acicle, and a less spiny merus on the cheliped for Surinam specimens.

Color.—Whitish, with large spines on inner margin of hand and carpus red; occasionally, hard parts lightly tinted with green or purple; eyestalks with a single band of black on white, and antennules with similar rings on ends of articles (Provenzano, 1959). In preserved material, these dark bands appear red (Holthuis, 1959).

Habitat.—Usually taken on hard or shelly bottom; shallow water to 20 fathoms.

Type locality.—Off Fort Jefferson Dock, Garden Key, Dry Tortugas, Fla.

Known range.—Reefs off Beaufort, N.C., to southern Florida; through West Indies to Surinam.

Remarks.—Ovigerous females have been reported from February to October in Florida (Provenzano, 1959, in part), in June in North Carolina, August in South Carolina, October in Puerto Rico, and in May from Surinam (Holthius, 1959).

Genus ***Clibanarius*** Dana, 1852

Dana, 1852, p. 6.

Clibanarius vittatus (Bosc). Striped hermit crab

Figure 97

Pagurus vittatus Bosc, [1801 or 1802], p. 78, pl. 12, fig. 1. *Clibanarius vittatus:* Hay and Shore, 1918, p. 410, pl. 30, fig. 9.—Provenzano, 1959, p. 371, fig. 5 D.

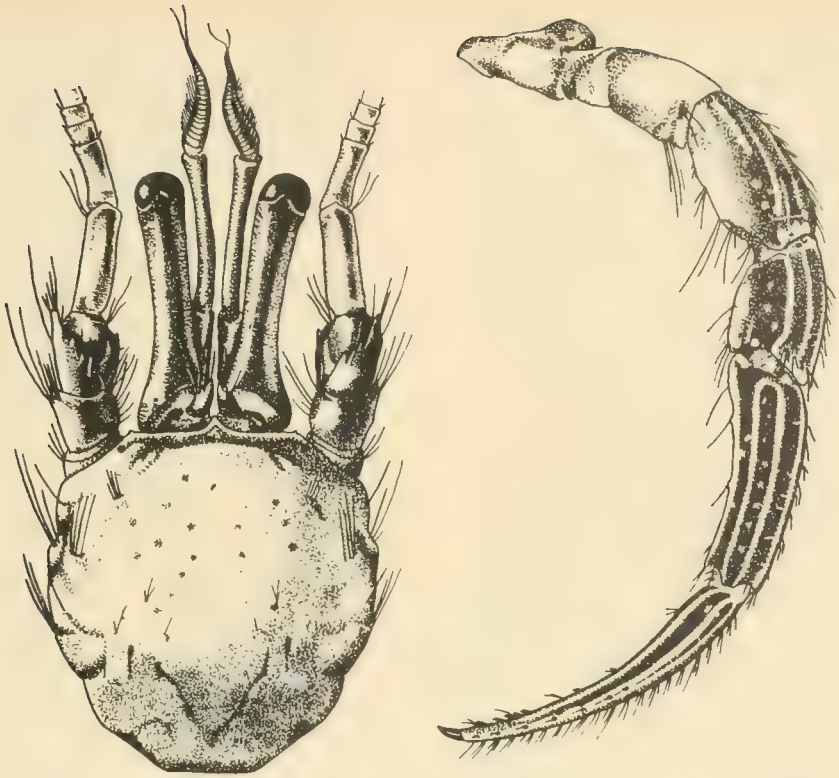

FIGURE 97.—*Clibanarius vittatus* (Bosc). A, anterior part of body in dorsal view, × 1.6; B, third leg, × 3.2 (after Holthuis, 1959).

Recognition characters.—Anterior shield of carapace subquadrate, a few fine hairs along lateral margin. Front with rostrum acute, triangular, slightly more prominent than lateral projections. Eyestalks almost as long as width of anterior shield, nearly cylindrical, cornea not dilated, right eyestalk occasionally slightly shorter than left; eye scales narrow, approximated at tips, but well separated at bases, margin with one to four spines, terminal largest. Antennular peduncles as long as eyestalks. Antennal peduncles reaching to at least three-fourths length of eyestalks; acicles acute, with three to five terminal spines, flagella reaching tips of walking legs.

Chelipeds equal, sparsely hairy; hands thick, inflated, twice as long as broad, covered thickly above, sparingly below, with somewhat blunted spines darker than color of hands and with bundles of stiff hairs springing from bases; fingers opening horizontally, heavy, toothed and somewhat gaping at base, cutting edges corneous, extending along upper side; carpus as long as palm. First and second walking legs exceeding chelipeds by over half length of dactyls, tips corneous; two distal articles with numerous bundles of hairs. Third and fourth walking legs reduced; third subchelate; fourth very small, chelate, and turned on back.

Measurements.—Length of carapace: male, 32 mm.; female, 29 mm.

Color.—Greenish to dark brown with longitudinal stripes of gray to white; antennular peduncles light above, dark laterally, with orange flagella; propodus of walking legs with four pairs of light, longitudinal stripes continuous with similar stripes on dactyl and carpus, one of ventral stripes usually somewhat diffuse (Provenzano, 1959).

Habitat.—Common on harbor beaches, especially on borders of mud flats (Pearse, Humm, and Wharton, 1942); often on rock jetties or high on bay shores (Whitten, Rosene, and Hedgpeth, 1950); waterline to a few feet.

Type locality.—Coasts of Carolina.

Known range.—Potomac River, Gunston, Va., to Rio de Janeiro, Brazil.

Remarks.—This large species is one of the commonest conspicuous hermit crabs of the shore region of the Carolina bays. It has a broad range along the western Atlantic, and Holthuis (1959) has given new distribution records, as well as a history of its early recognition in this hemisphere.

Ovigerous females have been reported from Surinam in July and August (Holthuis, 1959) and from Florida in October (Provenzano, 1959).

Genus *Petrochirus* Stimpson, 1858

Stimpson, 1858, p. 233 (71).

Petrochirus diogenes (Linnaeus)

Figure 98

Cancer Diogenes Linnaeus, 1758, p. 631.
Petrochirus bahamensis: Hay and Shore, 1918, p. 410, pl. 30, fig. 6.—Schmitt, 1935a, p. 206, fig. 66.—Provenzano, 1959, p. 378, fig. 8.—1961, p. 153 (rev.).
Petrochirus diogenes: Holthuis, 1959, p. 151 (rev.).

Recognition characters.—Anterior shield of carapace flattened, as broad as long, rough, uneven, and with scattered tufts of hairs; front trilobate, rostrum about as long as lateral projections. Eyestalks straight, dilated distally, with a tuft of hair above corneal surfaces and scanty tufts near base; eye scales broad basally, acute anteriorly with indistinct serrations. Antennular peduncles reaching or exceeding eyestalks. Antennal peduncles shorter than eyestalks; acicles slender, hairy, and minutely spined.

Chelipeds massive, subequal, right slightly larger; hands and carpi coarsely roughened with grouped tubercles separated by appressed setae on upper and, to some extent, lower surfaces, becoming spinose along inner margin; fingers opening obliquely, major chela with fingers tuberculate on crushing edges, minor chela with fingers somewhat spooned, cutting edges sharp, tips corneous. First two pairs of walking legs with carpus ornamented above like chelae; propodi similar with clusters of hairs beneath; dactyls with slightly twisted rows of spines and dense setae; propodi and carpi, especially of first walking legs, with dorsal row of dark-tipped spines. Third legs subchelate; last legs chelate and turned up against side.

Measurements.—Length of carapace: male, 75 mm.; female, 44 mm.

FIGURE 98.—*Petrochirus diogenes* (Linnaeus). Female in dorsal view showing well-developed triramous pleopods, × 0.35 (after Provenzano, 1959).

Color.—Generally reddish; chelipeds reddish except between fingers, and white spots on carpal articles; antennal and antennular peduncles longitudinally striped with red and white, antennal flagella transversely banded with red and white (Provenzano, 1959).

Habitat.—Mud, mud and shell, and sand bottoms. Common on shrimping grounds near Tortugas, Fla. (Provenzano, 1959), in the western Gulf of Mexico (Hildebrand, 1954, 1955), and on fishing grounds southeast of Cape Lookout, N.C., in about 18 fathoms; to 50 fathoms (Provenzano, 1959; Holthuis, 1959).

Type locality.—Near shores of Bahama Islands (Catesby, *in* Holthuis, 1959).

Known range.—Off Cape Lookout, N.C., to Brazil; West Indies.

Remarks.—The genus *Petrochirus* has a fossil record extending from the Cretaceous to the pres-

ent in North America (Rathbun, 1935). Toula (1911) considered the Miocene form from Panama to be conspecific with the living species in the West Indies region, but Rathbun (1918a) considered this form as distinct (*P. bouvieri*) and possibly ancestral to the modern species.

Petrochirus diogenes is the largest hermit crab in the Carolinian fauna and this feature, plus its coarsely tuberculate, ruddy appendages, makes it conspicuous. A common commensal is the porcellanid crab, *Porcellana sayana*, and other commensals on the shells carried by the crab, such as *Crepidula plana* (Say), bryozoans (*Scrupocellaria* sp.), tubicolous worms (*Hydroides* sp. and *Spirorbis* sp.) and other species, are mentioned by Pearse (1932b). Ovigerous females have been reported in March from the Virgin Islands (Provenzano, 1961).

Pearse (1932a) determined the freezing point of *P. diogenes* blood (range −1.90° to −2.32° C.).

Holthuis (1959) reviewed the complex nomenclatural history of the species, designated the type, restricted the type locality, and delimited the geographic range.

Genus ***Dardanus*** Paulson, 1875

Paulson, 1875, p. 96 (translation).—Hemming, 1958b, p. 163.—Provenzano, 1959, p. 372.

KEY TO SPECIES IN THE CAROLINAS

a. Propodus of second left walking leg conspicuously hairy, with a lateral longitudinal ridge paralleled by a groove, ridge crossed by rugae_____*venosus* (p. 123).

aa. Propodus of second left walking leg not hairy, without a lateral longitudinal ridge or groove, rugae arranged in herringbone pattern_____*insignis* (p. 124).

Dardanus venosus (H. Milne Edwards)

Figure 99

Pagurus venosus H. Milne Edwards, 1848, p. 61.

Dardanus venosus: Verrill, 1908, p. 441, text-figs. 58–59; pl. 26, figs. 4a, 5a.—Provenzano, 1959, p. 374, fig. 6 (rev.).

Recognition characters.—Anterior shield of carapace slightly longer than width of front, smooth, with few hairs and some deep lines near sides; anterior margin with rostrum wanting, lateral projections between bases of eyestalks and antennae prominent. Eyestalks stout, slightly constricted in middle, extending to tips of antennal peduncles or slightly beyond, a tuft of setae just behind cornea; eye scales widely separated, inner margins straight, blunt tips bearing several spines. Antennular peduncles exceeding cornea by one-third of terminal peduncular article. Acicles short, reaching midlength of eyestalks, armed with small, sharp spines.

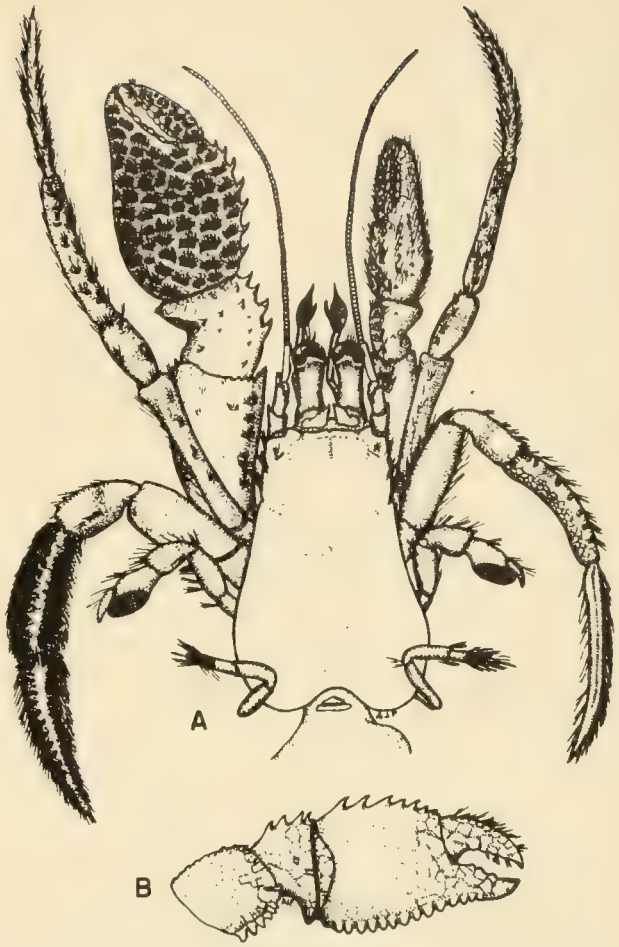

FIGURE 99.—*Dardanus venosus* (H. Milne Edwards). A, anterior part of body in dorsal view showing ridge on second left walking leg; B, inner surface of major chela showing "veins" which specific name describes; A–B approximately × 1.5 (after Provenzano, 1959).

Chelipeds unequal, left much larger than right; fingertips black, corneous, spooned. Major chela with outer surface covered by scalelike tubercles separated by fan-shaped fringes of appressed hairs, inner surface smooth, medial margin bearing row of seven sharp, horny-tipped spines continued as row of smaller spines on dactyl and as well-developed spines on carpus; carpus with smaller sharp spines scattered over surface. Minor chela narrower, lacking scalelike tubercles on outer surface, and with long setae rather than appressed bristles. Walking legs with dactyls

longer than propodi, longest in first pair; second left leg markedly different from others, with dactyl and propodus broadened, fringed with hairs, and with a lateral longitudinal ridge paralleled by a groove, ridge crossed with numerous rugae.

Measurements.—Length of carapace (medium sized individual) : 31 mm. (Verrill, 1908).

Color.—Walking legs with broad, transverse bands of red; legs, fingers of hands, and inside surfaces of chelipeds reticulated with fine red lines (hence, descriptive specific name) ; scalelike tubercles of hand and rugae of second left leg blue to purple; eye scales sometimes white (Provenzano, 1959).

Habitat.—Often found on sand and grass flats, on mud bottom, and in baited traps (various authors). Shells inhabited sometimes bear sponges or coelenterates (Holthuis, 1959). Shallow water near shore to 50 fathoms; rarely to 200 fathoms.

Type locality.—Guadeloupe.

Known range.—Off Beaufort Inlet, N.C. (Cerame-Vivas, Williams, and Gray, 1963); through West Indies to northeastern Brazil; Bermuda.

Remarks.—Ovigerous females have been reported from northeastern Florida in June, from the Virgin Islands in March and May (Provenzano, 1961), and from northeastern South America in April, May, July, and September.

Dardanus insignis (Saussure)

Figure 100

Pagurus insignis Saussure, 1858, p. 453, pl. 3, figs. 20, 20a.
Dardanus insignis: Verrill, 1908, p. 446, text-fig. 60; pl. 26, figs. 4 b, c, 5b.

Recognition characters.—Anterior shield of carapace longer than width of front, with scattered clumps of setae, and roughened slightly near anterior and anterolateral margins. Anterior margin with rostrum wanting; lateral projections on front triangular, thickened, prominent, and hairy on frontal edge. Eyestalks stout, slightly constricted in middle, extending almost to tips of antennal peduncles, a pencil of hairs at base of dilated cornea; eye scales prominent, well separated, serrated distally with a strong medial pair of spines separated from a smaller more lateral series of four spines by a notch obscured by a pencil of setae. Antennular peduncles with base of terminal article exceeded by eyestalks. Acicles

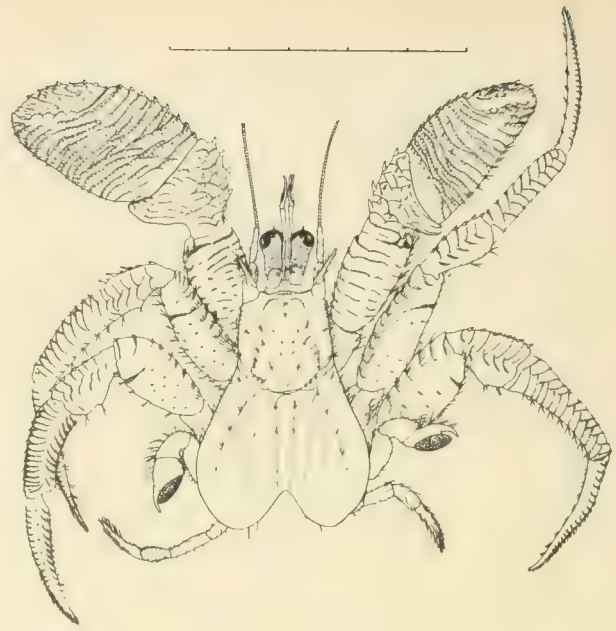

FIGURE 100.—*Dardanus insignis* (Saussure). Anterior part of male in dorsal view; 50 mm. indicated.

long, reaching to base of cornea, with a few spines and hairs arranged in a spiral line originating on inner surface at base and curving across dorsal surface to termination on lateral surface near tip.

Chelipeds heavy, left larger than right, covered with ciliated, tuberculate rugosities becoming bolder and more diagonal distally on hands and immovable fingers; movable finger of major chela with ciliated rugosities somewhat diagonal, those on minor dactyl irregularly arranged; opposed edges of fingers with heavy white teeth, tips black; spine on crest of meri, outer surface of carpi, and hands, largest spines on upper medial border; a row of spines on lower medial border of merus and ischium. First two pairs of walking legs strong, with rugose pattern similar to chelipeds and forming herringbone pattern on outer surface of propodus of large second left walking leg; dactyls of these walking legs with crest of spines dorsally, that of second left leg with crest of spines dorsally and ventrally, and continued below on propodus. Third and fourth walking legs reduced and specialized.

Measurements.—Male: length of carapace, 38 mm.; anterior shield, length, 17.5 mm., width, 15.5 mm.

Color.—Ground color yellowish; rugosities tan near body, becoming maroon on chelipeds and

first two pairs of walking legs distally, proximal rugae on hands with reticulate maroon pattern on yellowish background; anterior shield mottled tan; eyestalks banded alternately with maroon, yellow, and tan.

Habitat.—Fifteen to 124 fathoms.

Type locality.—Guadeloupe.

Known range.—Off Oregon Inlet, N.C., 17 fathoms (Cerame-Vivas, Williams, and Gray, 1963), to Port Aransas, Tex.; through West Indies to Guadeloupe.

Remarks.—Until recently this species was known only from beyond the 100-fathom curve in the Carolinas, but it has been collected in shallow water north of Cape Hatteras (Cerame-Vivas, Williams, and Gray, 1963).

Subfamily **Paguri**nae

The chief distinguishing characters for this group are given in the Key to Subfamilies of Hermit Crabs.

KEY TO GENERA OF PAGURINAE IN THE CAROLINAS

a. Fingers opening and closing horizontally; no paired appendages on abdomen of either sex.
  b. Vas deferens of male not protruding in form of a tube----------*Pagurus* (p. 125).
  bb. Vas deferens of left side protruding, and coiled in a spiral----------*Spiropagurus dispar* (p. 133).
aa. Fingers opening and closing obliquely; vas deferens of male not protruding; a pair of appendages on first abdominal segment of female only *Pylopagurus* (p. 133).

Genus *Pagurus* Fabricius, 1775

Provenzano, 1959, p. 393.—Hemming, 1958b, p. 163.

KEY TO SPECIES IN THE CAROLINAS

a. Eye scales unarmed or with single subterminal spine.
  b. Length of eyestalk not more than 3.5 times its greatest width.
    c. Width of major chela less than one-half length.
      d. Chelipeds subcylindrical, relatively smooth on outer surface; eye scales somewhat rounded distally, dorsal surface shallowly excavated *longicarpus* (p. 125).
      dd. Chelipeds not subcylindrical, relatively spiny on outer surface; eye scales rounded distally but not excavated on dorsal surface *defensus* (p. 127).
    cc. Width of major chela more than one-half length, one or both chelae broad and flattened.
      d. Dactyl of major chela with sharply produced angle on medial margin; no depressed spot at base of immovable finger of either chela *pollicaris* (p. 128).
      dd. Dactyl of major chela without sharply produced angle on medial margin; a depressed spot (or spots) at base of immovable fingers of chelae *impressus* (p. 129).
  bb. Length of eyestalk at least 4 times its greatest width----------*annulipes* (p. 130).
aa. Eye scales armed with two or more spines.
  b. Rostrum acute----------*pygmaeus* (p. 131).
  bb. Rostrum obsolete----------*brevidactylus* (p. 132).

Pagurus longicarpus Say

Figure 101

Pagurus longicarpus Say, 1817, p. 163.—Hay and Shore, 1918, p. 411, pl. 29, fig. 3.—Provenzano, 1959, p. 394, fig. 13 (rev.).

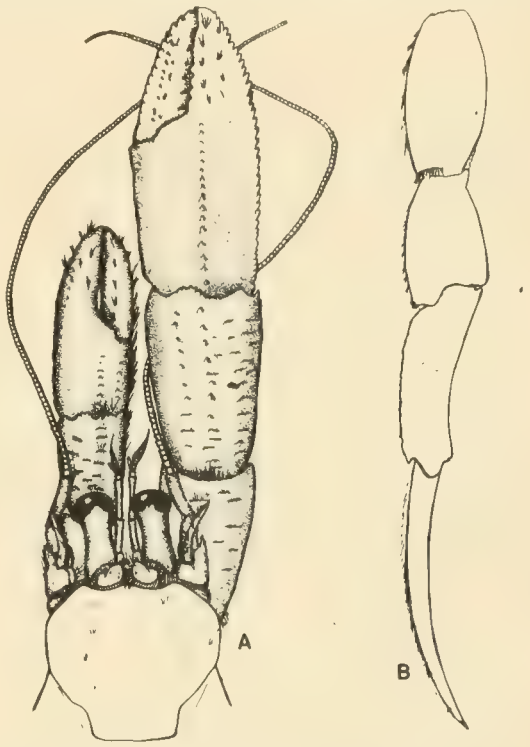

FIGURE 101.—*Pagurus longicarpus* Say. A, anterior part of body and chelipeds in dorsal view; B, second left walking leg in lateral view; A–B × 4 (after Provenzano, 1959).

Recognition characters.—Anterior shield of carapace subcordate, truncate posteriorly, about as broad as long. Rostrum obsolete, hardly as advanced as lateral projections of front. Eyestalks stout, 2–3 times longer than broad, much shorter than width of anterior shield, cornea dilated; eye scales with concave, oval anterior lobe armed with a subterminal spine. Antennular peduncles exceeding eyes by about half length of terminal article. Antennal peduncles exceeding eyes by

about one-third length of last article; acicles slender, curved sinuously outward, reaching to tip of cornea; flagella exceeding tip of major cheliped.

Right cheliped much larger and longer than left, subcylindrical, devoid of hairs except for a few short setae along inner edges of fingers; width of hand less than one-half total length, palm lightly crested and minutely dentate along outer margin, upper surface minutely granulate and with two incomplete rows of larger granules near proximal end; fingers short, hooked at tips; carpus as long as propodus to middle of finger, with two rows of subspinous tubercles and scattered smaller ones. Left cheliped smaller, hairier, similarly formed but relatively broader; fingers with cutting edges distally, gaping at base. First and second walking legs with dactyls longer than propodi, extending about as far as chelipeds. Third and fourth pairs of legs reduced in size, fourth turned upward on back.

Measurements.—Length of carapace: male, 10 mm.; ovigerous female, 11 mm.

Color.—Color varies with locality; specimens of west Florida are lighter than those of east coast; upper surface of chelipeds and all walking legs iridescent; posterior carapace light green; hand white with median diffused pigment stripe, carpus with dorsal stripe and one on each side; walking legs with dactyl unstriped, propodus with lateral stripe, merus with single lateral muddy brown stripe and transverse stripe from lower anterior margin to broad pigmented area on upper surface; antennae with dark bands alternating with shorter white bands. Young may have transverse band on each article of walking legs rather than stripe; lateral stripes of major cheliped with V-shaped appearance in dorsal view (Provenzano, 1959, from west Florida specimen).

Habitat.—Common on harbor beaches, in harbor channels, and in shallow littoral on a variety of bottoms; to 27.5 fathoms (possibly beyond).

Type locality.—"Inhabits Bay Shores" [east coast of United States].

Known range.—Minas Basin, Nova Scotia (Rathbun, 1929) to northern Florida; Sanibel Island, Fla., to coast of Texas (Provenzano, 1959; Whitten, Rosene, and Hedgpeth, 1950).

Remarks.—*Pagurus longicarpus* is one of the commonest decapod crustaceans in shallow water along the coast of the Eastern United States. Like other similarly available crustaceans, it has been the subject of a number of ecological and physiological studies, and these have been accomplished mostly around Woods Hole, Mass. Provenzano (1959) suggested that the Atlantic coast and Gulf of Mexico forms, with a hiatus between their ranges, may be subspecifically distinct.

The general habitat of *P. longicarpus*, summarized above, has been commented upon by other authors (Pearse, Humm, and Wharton, 1942; Allee, 1923). Allee concluded that the ubiquity of this hermit crab prevents it from being of aid in distinguishing shallow-water communities. Diatoms, detritus, and algae make up the food of this species (Sanders, Goudsmit, Mills, and Hampson, 1962).

The breeding season of this common form extends from early May to mid-September (Bumpus *in* Sumner, Osburn, and Cole, 1913b) in Massachusetts, and ovigerous females have been taken in January, March, and September in Florida (Wass, 1955, in part). Thompson (1901, 1903) described four zoeae, a glaucothoe, and a first postlarval stage, as well as various adolescent stages. He compared larval development of *P. longicarpus* with that of *P. annulipes* and gave remarks on the derivation and geological age of pagurids.

Autotomy and regeneration in this species received attention from Morgan (1900, 1901) and Haseman (1907), though investigations on this subject with other species now supersede the early studies. The first three pairs of legs have a fracture joint near their bases; hence, can be autotomized, but the last two pairs lack these and cannot be autotomized. Injuries distal to the fracture plane result in autotomy and regeneration; those proximal to the plane do not result in autotomy. Injured abdominal appendages are readily regenerated. Haseman carried this work farther, showing that when the chelipeds were removed at their breaking joints they differentiated from the tip proximally, but the first two pairs of clawed (walking?) legs differentiated from the base toward the tip. Direction of differentiation in the cheliped can be reversed by injuring the developing bud.

In another vein, conditioned and natural behavior of *P. longicarpus* has been the subject of a few

studies. Spaulding (1904) found the crab able to profit by experience in vision and taste experiments, and able to learn faster than *P. pollicaris*. Fink (1941) was able to demonstrate deconditioning of fear-reflex activity over a period of 18 days, the older crabs responding more slowly than young ones. Allee and Douglis (1945) found that a shell-less *P. longicarpus* would not feed, but if it were given a shell to occupy it would feed normally. Crabs in shells fight for food, the larger often fending smaller ones from a food supply. Movement from small to larger shells is accomplished only after several trials and thorough investigations of new shells, but shell-less crabs will accept almost any shape of shell in any condition. Shell-less crabs placed in a finger bowl tend to fight continuously until one or both are dead, usually within 24 hours. If an empty shell is dropped into a container with two shell-less crabs, one will immediately enter the shell. If the larger individual does not enter first, it will extract the smaller forcibly and enter in its place. Shell-less crabs will attack housed individuals regardless of size, but attackers were never seen to be successful when the two combatants were of equal size or when the housed individual was the larger.

Kropp and Perkins (1933) showed that in *P. longicarpus* and other remotely related decapods the chromatophore activity substance in the eyestalk will induce contraction of chromatophores in other species, and postulated that the substance is genetically similar throughout the group.

Finally, Reinhard (1944, 1945) and Reinhard and Buckeridge (1950) discussed parasitism in *P. longicarpus*. An examination of 8,000 crabs showed a 1-percent infestation with a larval acanthocephalid belonging to the genus *Polymorphus*. The worm was found in the abdominal cavity(?) usually attached to the hind gut or sometimes among tubules of the hepato-pancreas. The usual number of cysts per host was one, though as many as three occurred. Reinhard also described an entoniscid isopod, *Paguritherium alatum*, from this species. Entering the crab's body through the dorsal side of the eyestalk, and remaining in contact with this point of entry, the parasite elongates with but little damage to thoracic organs, but becomes greatly distended in the abdominal region. There it restricts the hepato-pancreas and nearly obliterates the gonads as it grows. Infestation does not externally modify the male host. In females, the parasite reduces size of the first three pleopods, especially length of the endopod, and causes partial or complete loss of ovigerous hairs on the external surface of the endopod and protopod. Thus, secondary sexual characters of the female crab are altered. One percent of the crabs investigated were infested with this parasite.

Pagurus defensus (Benedict)

Figure 102

Eupagurus defensus Benedict, 1892, p. 7.

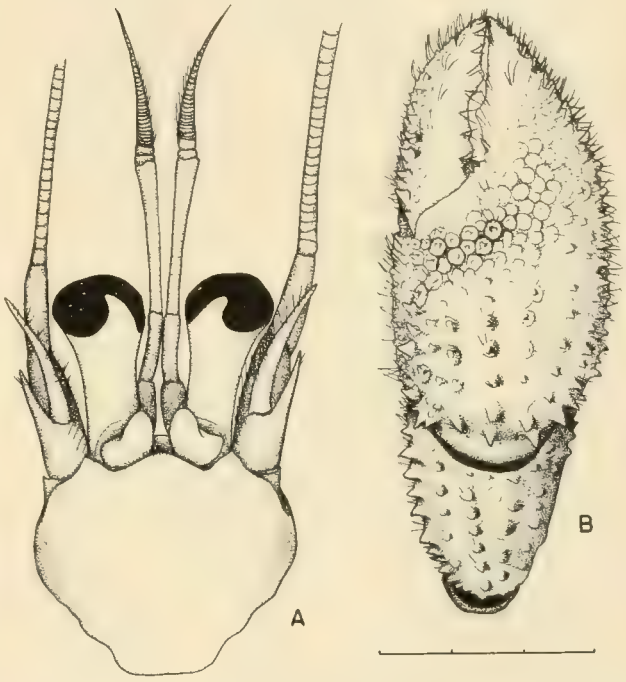

FIGURE 102.—*Pagurus defensus* (Benedict). A, anterior part of female in dorsal view; B, right chela, outer surface; 3 mm. indicated.

Recognition characters.—Anterior portion of carapace broader than long, subcordate. Rostral projection broadly rounded, lateral processes triangular, armed at apex with a short spine. Eyestalks stout, much dilated and flattened distally; eye scales broad, rounded, anterior margin forming a semicircle, armed with a subterminal spine. Antennular peduncles extending beyond eyestalks by two-thirds or more length of terminal article. Antennal peduncle extending beyond eyestalks by one-half length of terminal article; acicle curving outward and extending somewhat beyond eyestalk.

Chelipeds unequal, right larger than left. Major chela a little wider than carpus, fingers agape, margins set with comb of long, slender spines; upper surface with more or less diagonal rows of spines on palm and spines irregularly but closely set near base of dactyl and on immovable finger; dactyl with several rows of irregularly placed plates, and a small spine arising from center of each; carpus with three rows of sharp spines, one on outer margin, one on upper surface, and one on inner surface. Minor chela extending to base of major dactyl; hand armed with spines as in opposite member but hairier, and no spine-bearing plates on dactyl; fingers agape; carpus with a double crest of spines, outer margin convex, inner margin straight and flat; merus compressed. Walking legs long and slender, dactyls lightly setose, longer than preceding two articles together; propodus and carpus with a crest of spines.

Measurements.—Length of carapace: female, 7 mm.

Variations.—Fingers of the chelae do not gape in small individuals.

Habitat.—Sixteen to 49 fathoms.

Type locality.—Gulf of Mexico between Delta of Mississippi River and Cedar Keys, Fla., 30 fathoms.

Known range.—Cape Hatteras to Cape Lookout, N.C.; Tortugas, Fla., to Alabama.

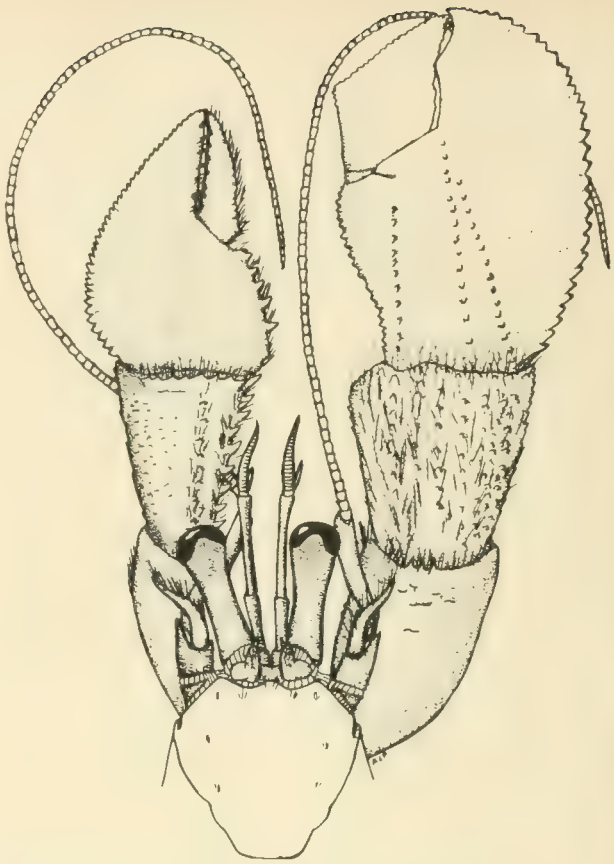

FIGURE 103.—*Pagurus pollicaris* Say. Anterior part of animal and chelipeds in dorsal view, approximately × 3 (after Provenzano, 1959).

Pagurus pollicaris Say

Figure 103

Pagurus pollicaris Say, 1817, p. 162.—Hay and Shore, 1918, p. 411, pl. 30, fig. 1.—Provenzano, 1959, p. 401, fig. 16 (rev.).

Recognition characters.—Anterior shield of carapace subcordate, nearly as long as broad, truncate posteriorly. Rostrum slightly less advanced than lateral projections of front. Eyestalks moderately stout, not so long as width of anterior carapace, nearly straight, cornea dilated; eye scales with round-tipped, slightly concave anterior lobe armed with inferior subterminal spine. Antennular peduncles exceeding eyestalks by approximately half length of last article. Antennal peduncles exceeding eyestalks; acicles slender, curved outward, reaching to or beyond base of cornea, hairy medially.

Chelipeds unequal, right much larger than left, both covered with small, closely spaced granules, outer margins with enlarged granules or small spines. Major chela stout, hand flattened; movable finger with prominent, projecting angle on medial border; tips of fingers acuminate; carpus with numerous tubercles, larger than on hand, subspinose and ciliated on upper surface; merus with a few squamiform tubercles. Minor chela with inner border dentate, movable finger not produced, dentation of inner border continued on inner dorsal border of carpus. First and second walking legs with dactyls much longer than propodi; first pair with small, well-defined spines along upper margin of propodus and carpus; second pair with spines reduced. Third legs reduced, fourth pair reduced and carried on back.

Measurements.—Length of carapace: male, 31 mm.; female, 27 mm.

Color.—Color varies with locality, those of west Florida being lighter than those of Northeastern States. Chelipeds basically white with gray margins on insides, tips of dactyls and dark area in

center of upper surface of each cheliped; remainder of body light gray-tan; eyestalks brown below cornea; hairs on antennules rusty brown (Provenzano, 1959, for west Florida form).

Habitat.—Deep channels of harbors and littoral waters; also found in shallow estuaries near ocean; near low-tide mark to 25 fathoms.

Type locality.—[East] coast of United States.

Known range.—Vineyard Sound, Mass., to northeastern Florida; Key West, Fla., to Texas (Provenzano, 1959).

Remarks.—Blake (1953) reported *P. pollicaris* from the Pleistocene of Maryland.

Ovigerous females have been reported in March from Florida (Provenzano, 1959). They have been found in January and November in North Carolina, and in April in Chesapeake Bay.

Pagurus impressus (Benedict)

Figure 104

Eupagurus impressus Bendict, 1892, p. 5.
Pagurus impressus: Provenzano, 1959, p. 399, fig. 15 (rev.).

Recognition characters.—Anterior shield of carapace about as broad as long, flattened. Rostrum much rounded, in line with somewhat more angular lateral projections of front. Eyestalks slender, about three times longer than greatest width, cornea dilated and flattened; eye scales with moderately slender, acuminate, slightly excavated anterior lobe, subterminal spine large. Antennular peduncles exceeding eyestalks by at least half of last article. Antennal peduncles slightly exceeding cornea; acicles curving outward, reaching to base of cornea, hairy on medial edge.

Chelipeds unequal, right much larger than left, upper surfaces dented, both covered with small, closely crowded granules, outer margins bearing enlarged granules or small spines. Dactyl of major cheliped with a rounded angle on medial border near tip followed by marginal spines or granules, tips of fingers acuminate; carpus with five longitudinal rows of small spines often obscured by irregularly arranged additional spines, a row of well-developed spines along inner edge. Minor cheliped reaching to angle of major dactyl; a row of spines along inner margin of hand and carpus; fingers somewhat spooned at tips, cutting edges well defined, tips corneous, dactyl with medial border tuberculate; carpus with several rows of small spines. First and second walking legs with dactyls much longer than propodi; first pair with row of small, well-defined spines along upper margin of propodus and carpus; second pair with spines reduced. Third legs reduced, fourth reduced and turned on back.

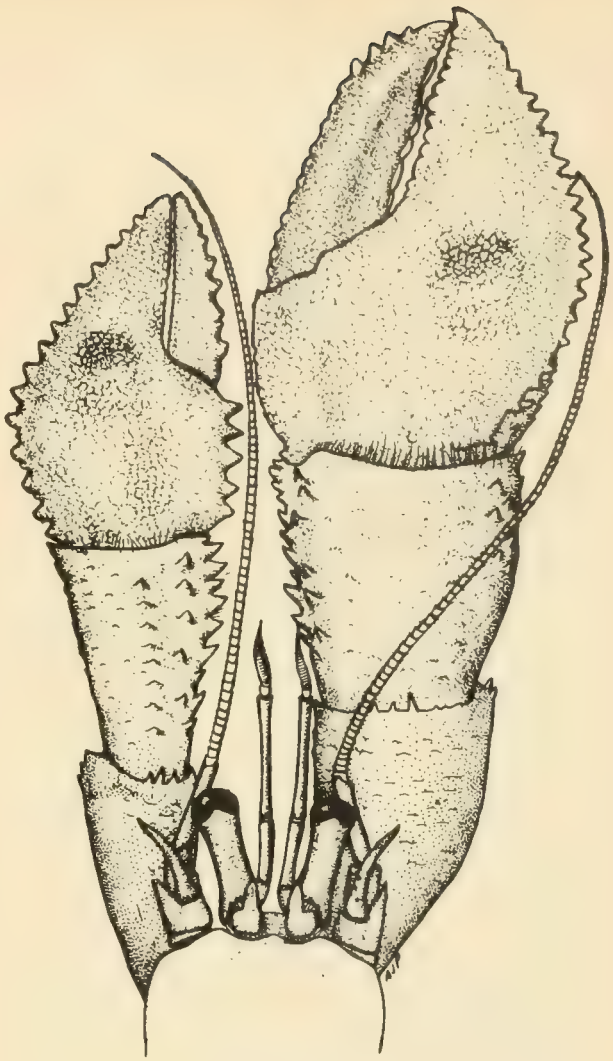

FIGURE 104.—*Pagurus impressus* (Benedict). Anterior part of body in dorsal view, approximately × 2.5 (after Provenzano, 1959).

Measurements.—Length of carapace: male, 25 mm.; female, 16 mm. (Provenzano, 1959).

Color.—Hands solid rust to chocolate brown, other appendages brownish with alternating thin bands of light color; antennae, antennules, and peduncles yellow; eyestalks brown above, bright blue below with bright scarlet at base of eyestalks (Provenzano, 1959).

Habitat.—On sandy bottom, grassy flats, or pilings; occasionally found in sponges (Wass, 1955); 6 to 18 fathoms.

Type locality.—Florida.

Known range.—Off Diamond Shoals, N.C., to east coast of Florida; western Florida from Sanibel Island north to vicinity of Alligator Harbor; Port Aransas, Tex.

Remarks.—Ovigerous females have been taken in January and February in the Carolinas.

Pagurus annulipes (Stimpson)

Figure 105

Eupagurus annulipes Stimpson, 1860a, p. 243.
Pagurus annulipes: Hay and Shore, 1918, p. 412, pl. 29, fig. 12 (rev.).—Provenzano, 1959, p. 407, fig. 18 (rev.).

Recognition characters.—Anterior shield of carapace subcordate, scarcely longer than wide, truncate posteriorly. Rostrum obsolete, about as long as rounded lateral projections of front. Eyestalks nearly straight, shorter than front, slightly constricted in middle, cornea not dilated; eye scales flat, broad, and rounded but with one or two spines on anterior border. Antennular peduncles exceeding eyestalks by about one-third of last article. Antennal peduncles reaching about to, or beyond, tip of eyestalks; acicles slender, curving outward, reaching about middle of last article of antennal peduncle; flagella exceeding major cheliped.

Chelipeds unequal, right much larger than left. Major cheliped long, subcylindrical, moderately and evenly granulate and ciliate above, except subspinose in large individuals; tips of fingers hooked, dactyl less than one-half length of hand; carpus nearly twice as long as broad, spinulose along inner margin. Minor cheliped much shorter, compressed, thickly ciliate and spinulose above; hand slightly shorter than carpus; fingers shorter than palm, with cutting edges distally, gaping at base. First and second walking legs with dactyls longer than propodi, legs slender, compressed; carpus with a distal spine on upper border. Third legs much reduced; fourth pair smaller, turned on back.

Measurements.—Length of carapace: male, 5 mm.; female, 4 mm. (Provenzano, 1959); Wass (1955) found a specimen with a carapace length of 7 mm.

Variations.—This is a small species. Males tend to attain larger sizes than females, and this is accompanied by a proportionately larger cheliped (Provenzano, 1959).

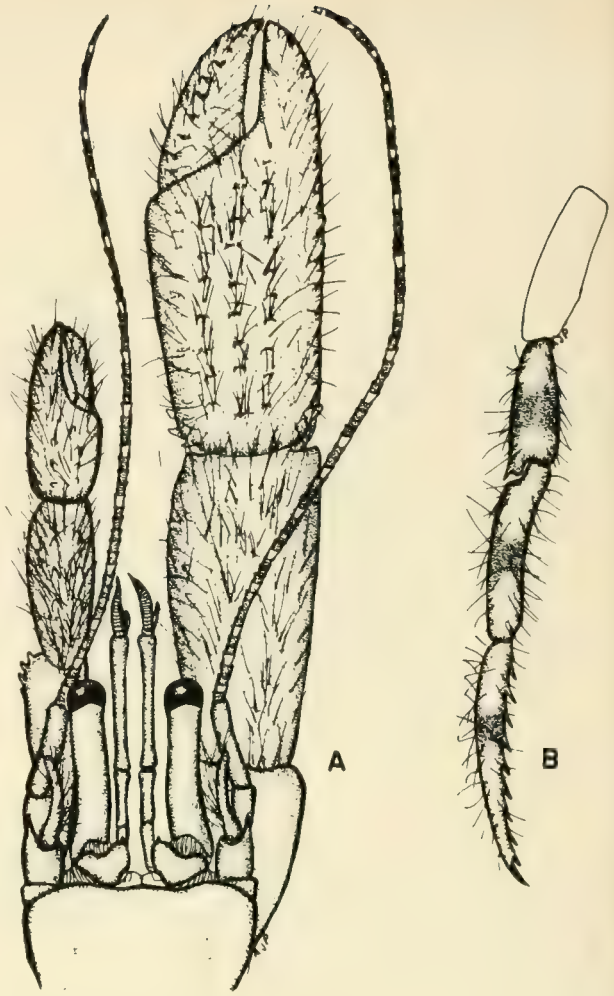

FIGURE 105.—*Pagurus annulipes* (Stimpson). A, anterior part of body and chelipeds in dorsal view; B, second left walking leg showing characteristic color bands in lateral view; A–B approximately × 7 (after Provenzano, 1959).

Color.—White to gray with brown pigment band around each article of walking legs; antennae with broad purple bands alternating with narrower white bands, occasionally with poorly defined longitudinal stripes on legs (Provenzano, 1959).

Habitat.—Fairly common on a variety of bottom types in Massachusetts, but not so common in the Beaufort Harbor area of North Carolina; abundant in *Thalassia* beds in southern Florida, seemingly preferring soft, sandy bottom to other

types; tolerates somewhat lowered salinities of estuaries; near low-tide mark to 23 fathoms (Schmitt, 1935a).

Type locality.—Beaufort Harbor, N.C.

Known range.—Vineyard Sound, Mass., around Florida peninsula to Alligator Harbor; Cuba; Puerto Rico.

Remarks.—Ovigerous females have been reported in September from Massachusetts (Thompson, 1903), and from February to April, and August to September in Florida (Provenzano, 1959). Thompson described four zoeal, a glaucothoe, a postlarval, and a number of adolescent stages at Woods Hole. The only difference he found between *P. annulipes* and *P. longicarpus* in larval development was the slightly smaller size of the former.

Pagurus annulipes may occur a few miles offshore, for it has been found in the stomachs of flounders (*Paralichthys dentatus*) taken 15 miles east-southeast of Oregon Inlet, N.C., in 20-fathom water along with numerous juvenile *Cancer irroratus*.

Pagurus pygmaeus (Bouvier)

Figure 106

Eupagurus pygmaeus Bouvier, 1918, p. 11, fig. 4.
Pagurus pygmaeus: Provenzano, 1959, p. 410, fig. 19.

Recognition characters.—Anterior shield of carapace longer than wide. Rostrum acute, slightly in advance of lateral projections, each bearing a terminal spine. Eyestalks shorter than width of anterior carapace, wide at base, tapering toward cornea; eye scales armed along medial margin with four or five spines. Antennular and antennal peduncles extending slightly beyond cornea; unarmed acicle reaching base of cornea.

Chelipeds unequal, right much larger than left, both with long but very fine hairs and forward-projecting spines. Major chela suboval, margin armed with strong spines, upper surface covered with smaller, nearly blunt spines; carpus with six very sharp spines on upper anteromedial surface, two additional spines more laterally placed, and a short row of spines along lateral margin. Minor chela much reduced, twice longer than broad, upper surface with many blunt spines, some forming two central rows; tips of fingers corneous, spooned; carpus with double row of large spines on upper surface. Walking legs with

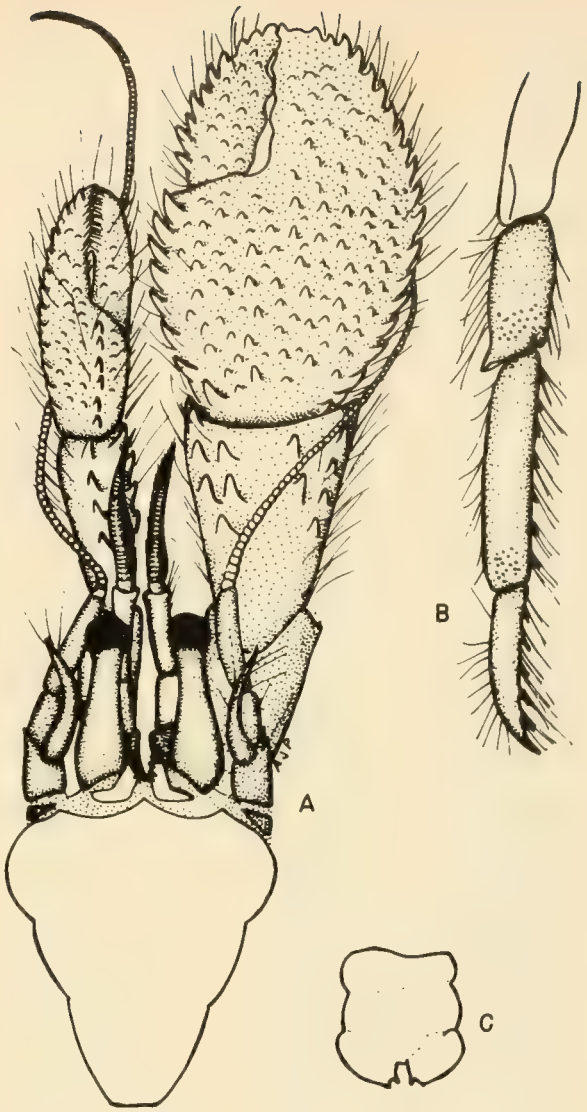

FIGURE 106.—*Pagurus pygmaeus* (Bouvier). A, anterior part of body and chelipeds in dorsal view; B, second left walking leg in lateral view; C, telson; A–C × 9 (after Provenzano, 1959).

dactyls shorter than propodi, approximately five ventrally placed spines in addition to terminal point, propodus with about seven less conspicuous spines, all articles with long sparse setae.

Measurements.—Length of carapace: male, 3 mm.

Habitat.—Shallow water to 45 fathoms.

Type locality.—"La baie de la Zocappa," near Santiago, Cuba.

Known range.—Off Little River, South Carolina; southern Florida to Puerto Rico.

Remarks.—The occurrence of this species in the Carolinas is open to question because identification of the South Carolina material is not certain. Nevertheless, the species is included here. The South Carolina specimens were ovigerous females taken in August.

Pagurus brevidactylus (Stimpson)

Figure 107

Eupagurus brevidactylus Stimpson, 1859, p. 91.
Pagurus brevidactylus: Provenzano, 1959, p. 413, fig. 20 (rev.).

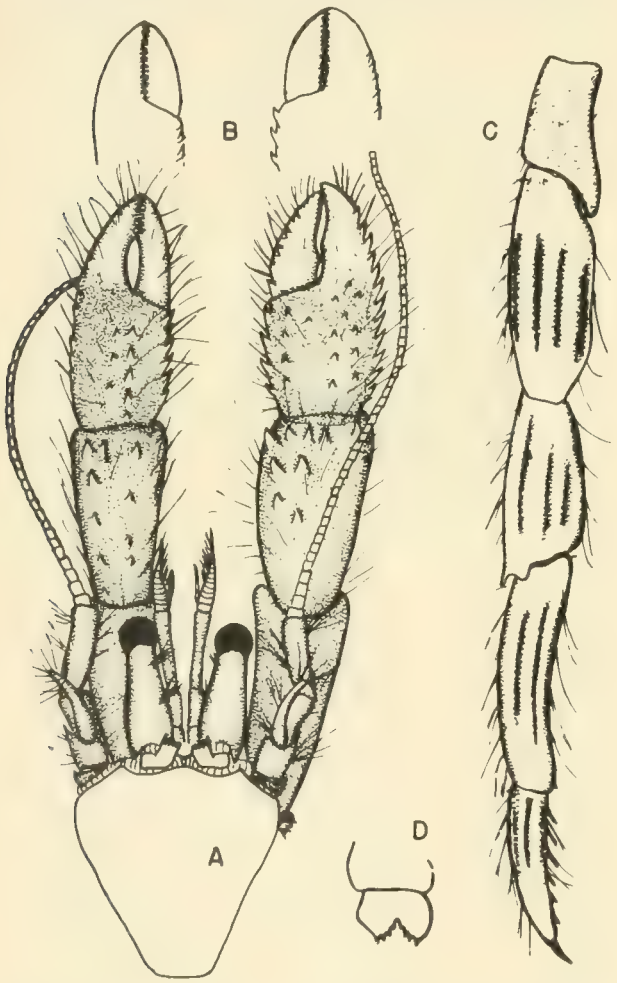

FIGURE 107.—*Pagurus brevidactylus* (Stimpson). A, anterior part of body and chelipeds, male in dorsal view; B, chelae of female in dorsal outline; C, second left walking leg in lateral view; D, telson; A–D approximately × 6 (after Provenzano, 1959).

Recognition characters.—Anterior shield of carapace slightly longer than broad. Rostrum obsolete and about on line with triangular lateral projections. Eyestalks swollen at base, tapering toward cornea; eye scales armed along anterior border with three to six spines. Antennular peduncles reaching at least to tips of eyestalks. Antennal peduncles slightly exceeding eyestalks; acicles reaching to base of cornea or slightly beyond.

Chelipeds unequal in males, right larger than left, equal or subequal in females; finger tips corneous, spooned. Hands covered with fine hairs, outer margin edged with spines, upper surface with smaller spines in several rows; carpi with strong spines above. Walking legs with long, fine, inconspicuous hairs; dactyls shorter than propodi and with five to eight conspicuous spines along inferior margin; propodi with only one or two inconspicuous spinules along inferior margin.

Measurements.—Length of carapace: male, 3 mm.; female, 4 mm.

Color.—Walking legs each characteristically colored with six rust-red, or maroon stripes on propodus, carpus, and merus, fewer on dactyl; stripes longitudinal and interrupted at ends of each article; ground color of walking legs yellow; hands brown with almost white fingers, not striped; carapace with scattering of red and white pigment in fresh specimens (Provenzano, 1959).

Habitat.—The species seems to prefer hard bottom in areas where water circulation is fairly good (Provenzano, 1959); has been taken from the Black Rocks in North Carolina; 1 to 125 fathoms.

Type locality.—Barbados.

Known range.—Off New River, N.C.; southwestern Florida from Anclote section southward; through West Indies to Barbados.

Remarks.—Provenzano (1959) called attention to the sexual dimorphism in this species. In females the hands are nearly the same size and the right hand is spooned and serrate along the inside margin of the fingers, whereas in males the right hand is not only the larger, but the finger tips appear more acuminate and the opposing margins of the fingers each bear a tooth. The specimens listed by Pearse and Williams (1951) as *P. bonairensis* are *P. brevidactylus* (U.S. National Museum notes).

Ovigerous females have been collected from June to August in North Carolina, March to August in Florida, and in April in Cuba.

Genus *Spiropagurus* Stimpson, 1858

Stimpson, 1858, p. 236.—Milne Edwards and Bouvier, 1893, p. 110.—Alcock, 1905, p. 117.

Spiropagurus dispar Stimpson

Figure 108

Spiropagurus dispar Stimpson, 1858, p. 236 [*nomen nudum*].—1859, p. 88.—Provenzano, 1961, p. 165.

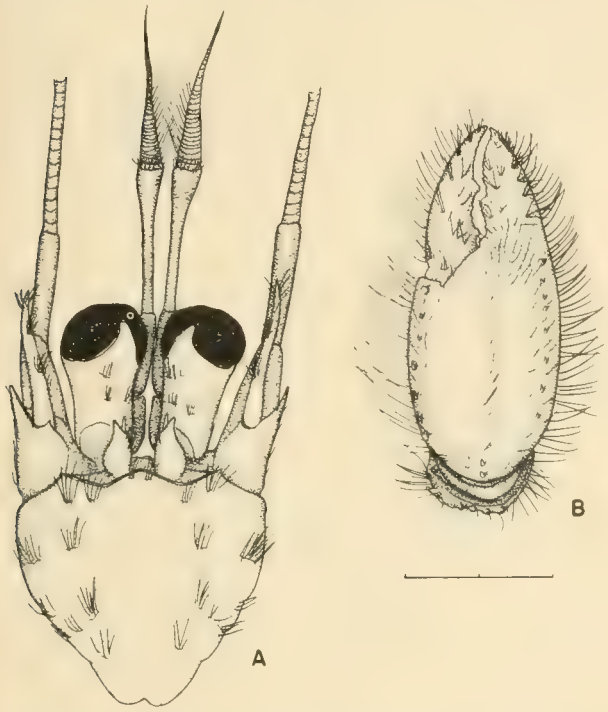

FIGURE 108.—*Spiropagurus dispar* Stimpson. A, anterior part of body in dorsal view; B, right chela, outer surface; 2 mm. indicated.

Recognition characters.—Carapace smooth but with hairy tracts on subcordate anterior shield and especially on anterior portion of membranous branchial areas; anterior margin with broadly rounded rostrum and equally advanced, acute lateral projections. Eyestalks more than twice as long as basal width, slightly exceeding proximal end of terminal articles of antennal and antennular peduncles, much dilated distally, cornea large; eye scales triangular, with abruptly narrowed acute tip directed slightly laterad, and slightly exceeded by strong subterminal spine. Acicles slender, longer than eyestalks.

Chelipeds elongate, setiferous, right chela larger than left. Major cheliped with fingers one-third to one-half length of palm, cutting edges of fingers toothed; palm ornamented with a dorsal, submarginal row of distinct spines on each side; carpus shorter than palm with scattered spines dorsally; merus with a single spine on internal anterior border, and a short row of spines on corresponding external border. Minor cheliped similar but narrower; palm less spiny, and fingers with a row of fine denticles on opposed edges. Anterior two pairs of walking legs elongate, slender distally, somewhat less pubescent than chelipeds; dactyls not dilated noticeably at base; carpi with a low crest of spines.

Left vas deferens of male prominent and coiled in a loose spiral.

Measurements.—Length of carapace: male, 5 mm.

Color.—Anterior carapace with three pairs of pigment spots, anterolateral vertical flaps light brown with a large, clear or colorless spot; cornea deep brown, eyestalks brown dorsally and ringed with brown near base; a narrow brown-orange ring at middle of fingers and at edge of immovable finger, hands reticulated with brown on upper surface; walking legs with a broad brown band on dactyls; propodi with a dorsal and ventral brown patch, a faint longitudinal lateral stripe, and a pair of dorsomedial brown patches; carpi with three faint stripes laterally (Provenzano, 1961, from specimen preserved in formalin).

Habitat.—The species has been found housed in *Natica canrena* Linné; 5 to 100 fathoms.

Type locality.—Barbados.

Known range.—Off South Carolina; Virgin Islands; Barbados.

Remarks.—Ovigerous females have been taken from the Virgin Islands in April and September (Provenzano, 1961).

Genus *Pylopagurus* Milne Edwards and Bouvier, 1893

Milne Edwards and Bouvier, 1893, p. 74.

KEY TO SPECIES IN THE CAROLINAS

a. Large chela almost smooth on upper surface, border finely crenulate; abdomen straight—*discoidalis* (p. 134).
aa. Large chela more or less tuberculate on upper surface, border definitely toothed; abdomen coiled.
  b. Outer surface of chelae nearly flat, not conspicuously tuberculate; rostrum exceeding unarmed lateral projections of front—*corallinus* (p. 134).
  bb. Outer surface of chelae conspicuously convex, conspicuously tuberculate; rostrum about equal to prominent minutely armed lateral projections of front—*rosaceus* (p. 135).

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Pylopagurus discoidalis (Milne Edwards)

Figure 109

Eupagurus discoidalis Milne Edwards, 1880, p. 41.
Pylopagurus discoidalis: Milne Edwards and Bouvier, 1893, p. 76, pl. 6, figs. 7–14.

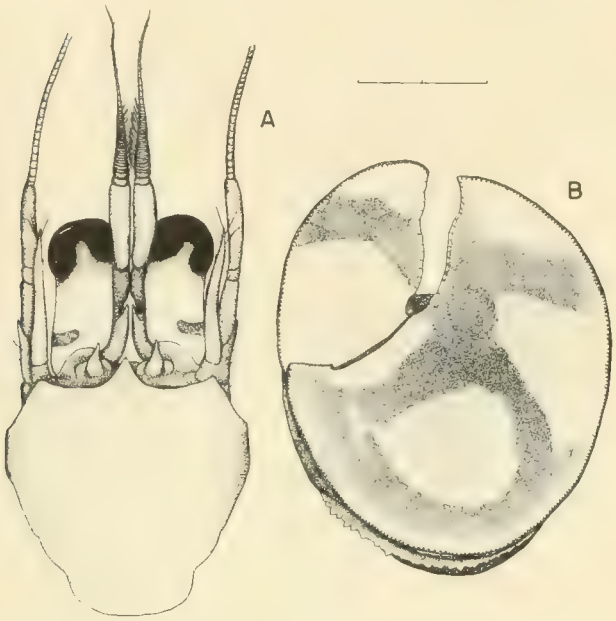

FIGURE 109.—*Pylopagurus discoidalis* (Milne Edwards). A, anterior part of ovigerous female in dorsal view, eyestalks showing color pattern; B, right (major) chela of ovigerous female, upper surface showing color pattern; 2 mm. indicated.

Recognition characters.—Anterior shield of carapace strongly calcified, subcordate, truncate posteriorly; anterior margin with large, sharp-pointed rostrum extending beyond middle of eye scales; lateral projections low and rounded, borders lateral to them very oblique. Eyestalks short, thick, widest distally, much shorter than length of frontal border, slightly exceeding acicles but not reaching middle of terminal article of antennular and antennal peduncles, cornea large; eye scales narrow, lanceolate. Acicles without spines and deflected somewhat outward.

Chelipeds unequal, right larger than left. Major chela in form of operculum adapted to close openings in *Dentalium* shells or similar tubes. Chela flexing at right angle on carpus and incapable of complete extension; upper surface smooth, flattened, or slightly excavated, nearly discoidal in outline, surrounded by a raised, finely crenulate border; lower surface slightly wrinkled with lines; fingers compressed, internal border of dactyl with rounded tubercles; carpus short, dilated in front, external surface ornamented with granulations following feebly squamose, irregular lines (occurring also on hand, back of edge forming operculiform portion), and with a few denticles on anterior border. Minor cheliped shorter than right one; chela oval, with very fine denticles on external border; fingers agape at base, and terminating in corneous tips; carpus with some spines on crest. Walking legs reaching tip of major chela, dactyls lanceolate with corneous terminal claw well developed.

Measurements.—Length of carapace: male, 11 mm.; female, 10 mm.; sexual maturity attained at cephalothorax length of 4–5 mm.

Variations.—The large chelae become more discoidal with advancing age (Milne Edwards and Bouvier, 1893).

Color.—Whitish but with large areas of reddish on hands, on each article of legs, and a ring of same color near base of eye; reddish color may extend over anterior portion of cephalothorax (Milne Edwards and Bouvier, 1893).

Habitat.—The species has been taken from *Dentalium* shells and from annelid tubes of similar shape; 30 to 508 fathoms.

Type locality.—Montserrat, 120 fathoms.

Known range.—Off North Carolina capes, through eastern Gulf of Mexico and West Indies to mouth of Amazon River, Brazil (Provenzano, 1963).

Remarks.—Ovigerous females have been recorded in November from southern Florida and Brazil.

Pylopagurus corallinus (Benedict)

Figure 110

Eupagurus corallinus Benedict, 1892, p. 23.
Pagurus corallinus: Hay and Shore, 1918, p. 412, pl. 30, fig. 4.

Recognition characters.—Anterior shield of carapace subcordate, truncate posteriorly. Rostrum obtuse, produced beyond rounded, unarmed, lateral projections of front. Eyestalks stout, falling far short of tip of antennular peduncle, largest distally, cornea dilated; eye scales sharp pointed, and with a prominent subterminal spine. Antennal peduncle nearly as long as that of antennule; acicle reaching nearly to tip of cornea.

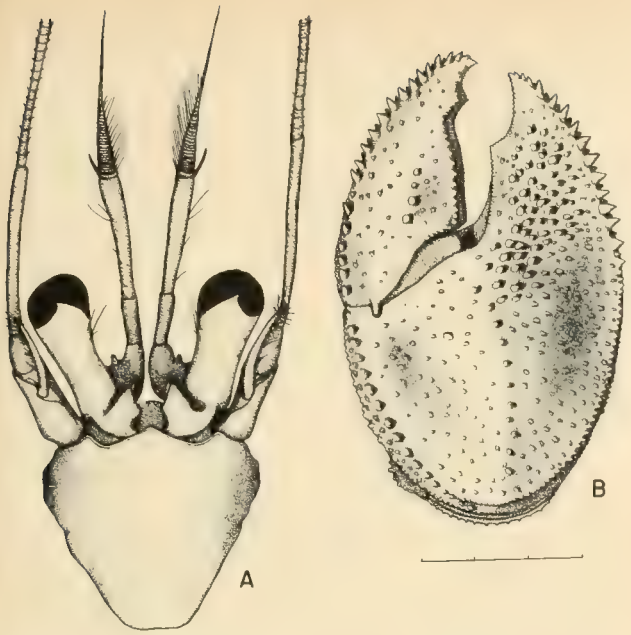

FIGURE 110.—*Pylopagurus corallinus* (Benedict). A, anterior part of body in dorsal view; B, right chela, outer surface; (from two specimens) 3 mm. indicated.

Chelipeds unequal, right larger than left. Upper surface of major chela flattened or slightly excavated, covered with small, slender spines becoming flattened and mushroom-shaped on immovable finger; hand fringed with spines, often alternately large and small, becoming longer near tips of fingers, inner surface with spinose tubercles between base of dactyl and recess receiving carpus, recess bounded by crest; carpus approximately as long as palm, upper surface thickly set with sharp, spiny granules, margin with rows of small spines; merus compressed, quadrilateral when viewed laterally. Minor chela with hand broad, compressed; fingers broad, gaping at base; carpus compressed, and surmounted by an inner row of small and an outer row of larger spines; merus compressed. Carpus and propodus of first walking leg, and carpus of second, crested with acute spines.

Measurements.—Length of carapace: male, 7 mm.; ovigerous female, 5 mm.

Color.—Large cheliped with merus and carpus blotched red and white; small cheliped and walking legs banded with same colors (Benedict, 1892).

Habitat.—In tunicates, stony corals, and bryozoans; 21 to 56 fathoms.

Type locality.—Off Key West, Fla.

Known range.—Off Cape Lookout, N.C., to Gulf of Mexico between Cedar Keys, Fla., and Mississippi Delta; off Cape Catoche, Yucatan, Mexico.

Remarks.—Ovigerous females have been taken off South Carolina in March, and southern Florida in June.

Pylopagurus rosaceus Milne Edwards and Bouvier

Figure 111

Pylopagurus rosaceus Milne Edwards and Bouvier, 1893, p. 97, pl. 7, figs. 10–17.—Hay and Shore, 1918, p. 413, pl. 30, fig. 5.

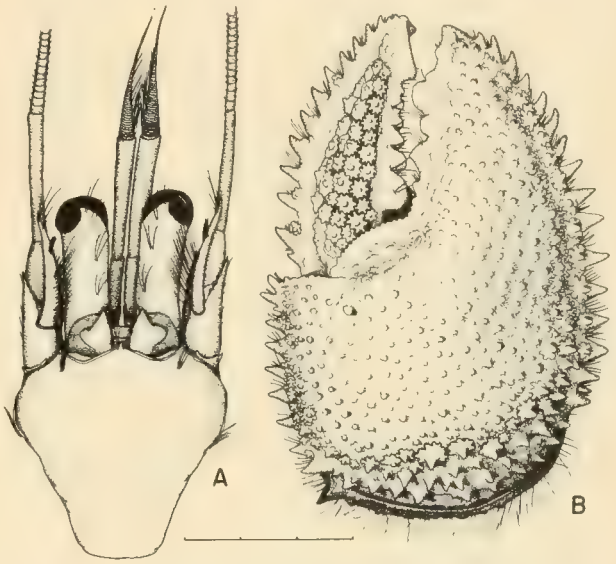

FIGURE 111.—*Pylopagurus rosaceus* Milne Edwards and Bouvier. A, anterior part of body in dorsal view; B, right chela, outer surface with detail shown only on dactyl; (from two specimens) 3 mm. indicated.

Recognition characters.—Anterior shield of carapace subcordate, somewhat truncate posteriorly; anterior margin with three projections, rostrum obtuse and slightly advanced beyond strong lateral projections, each terminating in a minute spine; sides of dorsal surface and anterior surface with a few tufts of setae. Eyestalks stout, considerably shorter than anterior shield, distinctly dilated distally, and with three or four pencils of setae in line along upper surface; eye scales acute anteriorly, each ending in an acute, subterminal spine. Antennal peduncle extending beyond eye, flagellum slender and longer than body; acicle strongly curved, reaching almost to distal edge of cornea.

Chelipeds unequal, right much larger than left. Both chelae capable of being bent down at a right angle to carpus to form, either singly or together, an operculum closing orifice of cavity inhabited by crab. Both margins of major chela, and outer margin of minor one, armed with a row of close-set, conical teeth; upper surface of both covered with closely crowded, rosettelike tubercles, each consisting of a central larger tubercle surrounded by a number of smaller ones; inner surface of major hand nearly smooth between base of dactyl and recess receiving carpus. Carpus of major cheliped with scattered sharp spines and hairs dorsally; merus with cross striae on upper surfaces and with anterior edges serrated with teeth in a single row. Minor cheliped similar but hairier and with a crest of spines on carpus. Walking legs of medium length, first and second of left side, and second of right side, exceeding large chela.

Measurements.—Length of carapace: male, 9 mm.; female, 10 mm.

Habitat.—The type was taken from an unknown species of the molluscan genus *Antillophos* (=*Phos*); 65 to 92 fathoms.

Type locality.—Grenada, 92 fathoms.

Known range.—South of Cape Lookout, N.C.; off Western Dry Rocks, Key West, Fla.; Grenada, and Surinam.

Remarks.—An ovigerous female has been taken from the Surinam locality in September.

Superfamily **Hippidea**

Abdomen reduced in size, bent under thorax; appendages of sixth segment not adapted for swimming. First pair of legs simple or subchelate, second to fourth legs with last article curved and flattened. Rostrum small or wanting. Third maxillipeds without epipodites.

Family **Albuneidae**

Carapace flattened and without wings covering legs. First pair of legs subchelate. Third maxillipeds narrow. Telson not conspicuously lengthened, almost oval.

KEY TO GENERA IN THE CAROLINAS

a. Eyestalks narrow, triangular_____*Albunea* (p. 136).
aa. Eyestalks broad, oval_____*Lepidopa* (p. 138).

Genus ***Albunea*** Fabricius, 1798

Gordon, 1938, p. 190.

KEY TO SPECIES IN THE CAROLINAS

a. Dactyl of second and third legs with blunt, rectangular lobe at base of anterior border_____*gibbesii* (p. 136).
aa. Dactyl of second legs with asymmetrically mucronate spur, and third legs with acute, falciform spur at base of anterior border_____*paretti* (p. 137).

Albunea gibbesii Stimpson

Figure 112

Albunea symnista Gibbes, 1850, p. 187.
Albunea gibbesii Stimpson, 1859, p. 78, pl. 1, fig. 6.—Benedict, 1901, p. 139.—1904, p. 625.—Hay and Shore, 1918, p. 414, pl. 30, fig. 11.—Schmitt, 1935a, p. 208.—Gordon, 1938, fig. 3e, p. 192, fig. 4b, p. 194.

Recognition characters.—Carapace about as broad as long, convex from side to side, nearly straight from front to back; front with a minute rostrum, and at either side a strong spine followed by 7 to 10 slender spines; anterolateral angle with a stout conical spine below *linea anomurica* projecting little if any beyond anterior border; posterior margin deeply and broadly notched; dorsal surface with numerous, irregular, more or less transverse, impressed lines, a short ciliated one near front, and one crossing near middle in shape of spread M being most conspicuous.

Eyestalks narrow, triangular, cornea at tip minute. Antennules about twice as long as carapace; flagella slender and densely ciliated above and below along inner surface, forming respiratory tube when approximated. Basal article of antenna with an acute, small, lateral spine; flagellum about half as long as peduncle. First pair of legs stout, hairy, all but distal articles inflated; hand subchelate; inferior distal angle of propodus produced into a spine; dactyls curved and rather slender. Second, third, and fourth legs stout, hairy, and with falcate dactyls; dactyl of third leg with falciform spur at base of anterior border, and second with similar broader spur. Fifth legs weak, borne above others.

Second, third, and fourth abdominal segments with expanded pleura, fifth and sixth segments small. Female with long uniramous pleopods on second to fifth segments. Uropods consisting of a rather large basal article and two small falcate blades. Telson of male triangular, of female rounded.

Measurements.—Length of carapace: male, 16 mm.; female, 20 mm.

Variations.—There is some individual variation in the pattern of spines on the anterior margin of the carapace. Spines may vary in number, be single, or occasionally be so close together as to appear doubled.

Color.—Light brown to orange tan above, cross striae lighter, with irregularly placed iridescent areas; antennules with alternating light and dark bands; eyestalks with a white ring behind cornea; underparts light (from recently preserved specimens). Light purple with whitish markings, more or less iridescent (various authors).

Habitat.—Sandy bottoms; extreme low-tide mark to 35 fathoms.

Type locality.—St. Augustine, Fla. (Stimpson); Sullivans Island, S.C. (Gibbes).

Known range.—East of Cape Lookout, N.C., to Texas; through West Indies to São Sebastião, São Paulo, Brazil.

Remarks.—*Albunea gibbesii* is occasionally found on sandy shoals, especially at times of extremely low tides when heat from the sun warms the exposed sand and drives the animals to the surface. Occasional specimens are found by digging, and specimens have been taken in both the Carolinas by dredging to depths of 35 fathoms.

Ovigerous females have been taken in North Carolina in June.

Pearse, Humm, and Wharton (1942) showed that *A. gibbesii* burrows backward into the sand as do the similar highly specialized sand dwellers, *Lepidopa websteri* and *Emerita talpoida.* These authors stated that *A. gibbesii* scrapes food from the setose antennules with the mouth parts; however, the chelate first legs and well-developed mandibles suggest feeding habits more like those of *Lepidopa* species. The function of the antennules as a possible feeding device was discussed by Benedict (1904).

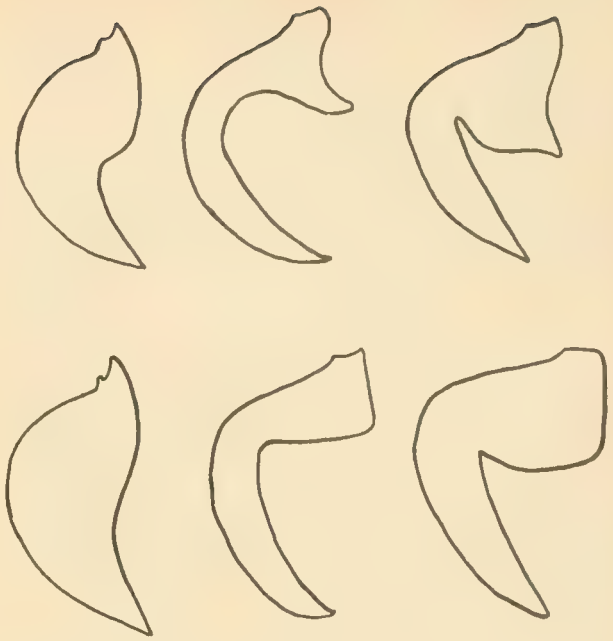

FIGURE 112.—Dactyls of second to fourth legs (from right to left); upper row, *Albunea paretii* Guérin; lower row, *Albunea gibbesii* Stimpson (after Gordon, 1938).

Albunea paretii Guérin.

Figures 112–113

Albunea oxyophthalma Leach (MS) *in* White, 1847b, p. 57 (*nomen nudum*).

Albunea paretii Guérin, 1853, p. 48, pl. 1, figs. 10–10a.

Albunea paretoi: Monod, 1956, p. 37, figs. 2–9 (rev.).

Recognition characters.—Similar to *A. gibbesii*, differing chiefly in characters given in key; dactyl of second legs with asymmetrically mucronate spur, third legs with acute, falciform spur at base of anterior border.

FIGURE 113.—*Albunea paretii* Guérin. Animal in dorsal view, legs of left side not shown, 5 mm. indicated.

Measurements.—Length of carapace: female, 20 mm.

Habitat.—Sandy bottom; low-tide mark to 21 fathoms.

Type locality.—[Uncertain], America.

Known range.—Beaufort Inlet, N.C., to Corpus Christi, Tex.; through West Indies to near mouth of Amazon River, Brazil; Bermuda; Cape Verde Islands and Senegal to Gold Coast, West Africa.

Remarks.—Monod (1956) reviewed the tangled history of the names given this species, but emended the specific name to conform to the name of the donor of the type specimen, Marquis of Pareto. Since Guérin used the spelling *paretii* twice in the original description, this spelling must be regarded not as a printer's error but as intentional (Holthuis, personal communication).

Ovigerous females have been taken in June in North Carolina.

Genus ***Lepidopa*** Stimpson, 1858

Stimpson, 1858, p. 230.—Holthuis, 1960a, p. 27 (rev.).

Lepidopa websteri Benedict

Figure 114

Lepidopa venusta: Kingsley, 1880, p. 410.
Lepidopa websteri Benedict, 1903, p. 892, fig. 3.—Hay and Shore, 1918, p. 415, pl. 30, fig. 12.

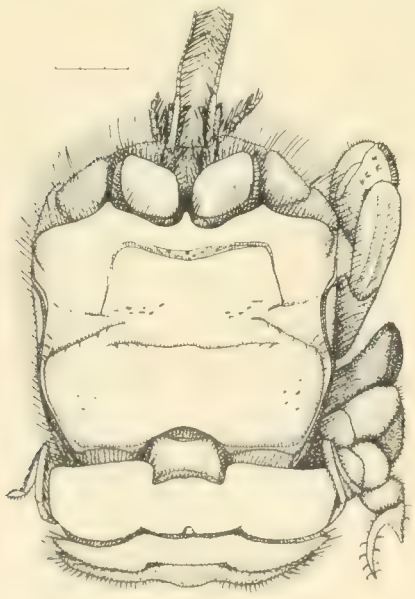

FIGURE 114.—*Lepidopa websteri* Benedict. Animal in dorsal view, first to fourth legs of left side not shown, 5 mm. indicated.

Recognition characters.—Carapace about as broad as long; front fringed with setae, produced into a short, triangular rostrum with acuminate tip, and to either side of it a broadly triangular lateral projection with acuminate tip slightly more advanced; margin between base of rostrum and each lateral projection almost straight; anterolateral angle produced into a flat spine above *linea anomurica;* sides sinuous and slightly convergent posteriorly, folded inward ventrally over bases of legs, more or less membranous posteriorly; dorsal surface crossed near front by an impressed, ciliate band with ends directed posteriorly, a narrower interrupted band ending in obliquely impressed lines crossing at about middle of carapace; posterior margin concave at middle.

Eyestalks irregularly oval, lamellate. Antennules with peduncles exceeding eyestalks; flagella straight, slender, nearly three times as long as carapace, fringed with hairs, and forming a respiratory tube when approximated. Antennae inserted at extreme outer angles of front, basal article stout; antennal scale reduced to a minute point; flagellum stout, curved, composed of seven short joints. First legs with broad, flat articles; dactyl turned back on propodus to form subchela. Second, third, and fourth legs with terminal joint bifurcated. Fifth legs much reduced, slender, and folded.

Abdomen short and partly flexed beneath thorax; second, third, and fourth segments with expanded pleura. Uropods small, with slender basal article, and long, oval blades, their margins and those of abdominal segments fringed with long, silky hairs. Telson cordate.

Measurements.—Length of carapace: 12 mm.

Color.—All parts white, iridescent, with pink being most conspicuous tint on anterior part of carapace, and blue showing along sides, in depressions of carapace, and on extremities of fifth legs; dorsal plates of abdomen faintly pink tinged, bordered by a delicate blue green; on either side of middorsal line, pink shading into red, and blue becoming deeper in shade (from note by A. Shaftsbury, U.S. National Museum records).

Habitat.—Usually found on gradually sloping sand beaches of open ocean at or immediately below low-tide mark (Pearse, Humm, and Wharton, 1942); shallow water, limits unknown.

Type locality.—Beach near Fort Macon, [Carteret County], N.C.

Known range.—Drum Inlet to Beaufort Inlet, N.C.; Ship Island and Petit Bois Island, Miss.

Remarks.—Knowledge of the ecology of this species is confined to the brief account given by Pearse, Humm, and Wharton (1942) which included detailed drawings of the specialized legs, as well as a lateral view of the whole animal. The species is highly adapted for burrowing in sand, and is usually found in small numbers. It burrows backward, and at rest lies at an angle to the surface with the long antennules extended in the water above. If disturbed, the animals may descend several centimeters into the sand. Benedict (1904) commented on the possible feeding function of the antennules in the genus *Lepidopa*. In 1903, he found setae of annelids, skin of a small *Synapta*, and parts of the flagella of some small crustaceans among stomach contents of *Lepidopa scutellata*. Such finding would be in accord with the fact that *Lepidopa*, like *Albunea*, has well-developed mandibles (Snodgrass, 1952).

Ovigerous females have been taken in July, and juveniles taken in plankton tows in July and August in North Carolina.

Family **Hippidae**

Carapace subcylindrical, and with wings covering legs. First legs simple. Third maxillipeds broad. Telson lengthened, lancet-shaped.

Genus ***Emerita*** Scopoli, 1777

Heegaard and Holthuis, 1960, p. 181.

KEY TO SPECIES IN THE CAROLINAS

(After Schmitt, 1935a)

a. Dactyls of first legs subacute or sharply pointed distally; transverse rugosities more or less continuous over dorsum and continued posteriorly to inferior margin of carapace wings_____*benedicti* (p. 139).

aa. Dactyls of first legs rounded or obtuse distally; lateral expansions or wings of carapace for greater part smooth and punctate_____*talpoida* (p. 140).

Emerita benedicti Schmitt

Figure 115

Emerita benedicti Schmitt, 1935a, p. 215, figs. 71 a, b.—Lunz, 1939, p. 336.

Recognition characters.—Body convex, oval; carapace firm; transverse rugosities more or less continuous, close set, and crossing whole of dorsum, those on posterior part continued on wings of carapace to inferior margin. Rostrum equilaterally triangular in shape, separated by a rounded sinus on each side from a prominent and subacute tooth; an impressed, transverse line behind rostrum and a deeper, more strongly curved one farther back. Posterolateral margins extending downward to cover bases of legs; anterolateral margins concave and subserrate.

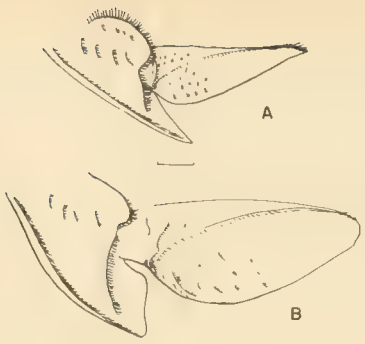

FIGURE 115.—Dactyl and portion of propodus of first leg; A, *Emerita benedicti* Schmitt; B, *Emerita talpoida* (Say); 1 mm. indicated.

Eyestalks long, slender; cornea minute. Antennules about three times length of eyestalks; basal article with flagella hairy, forming respiratory tube when approximated. Antennae normally held beneath third maxillipeds, nearly twice as long as carapace when extended; first peduncular article short, second one largest, with outer margin produced into a strong superior, and much longer inferior, spine, both exceeding eyestalks; flagellum densely beset laterally with eight rows of fringed setae, outer rows longest.

First pair of legs directed forward, articles more or less hairy, and with impressed, interrupted, transverse ciliated lines; dactyl subacute distally; fifth article spinose distally. Second, third, and fourth legs less strong, hairy, tips curved and foliaceous. Fifth legs almost filamentous, entirely concealed beneath abdomen.

Abdomen broadest anteriorly, narrow posteriorly, flexed so that telson and sixth segment lie beneath body. Uropods turned forward, resting along sides of proximal segments. Telson elongate, lanceolate, margined with reflected setae above and inflected ones on edge; base with two short, impressed lines.

Measurements.—Length of carapace: ovigerous female, 18 mm.

Habitat.—Shell bottom, and probably other types (Lunz, 1939); to 2 fathoms.

Type locality.—Tampa Bay, Fla.

Known range.—Type locality, and Folly River to Edisto Island, Charleston County, S.C.; Gulf coast of Texas.

Remarks.—Lunz (1939) reported ovigerous females from South Carolina in June, and they are also known from there in July.

Emerita talpoida (Say). Mole crab; sand bug

Figures 115–116

Hippa talpoida Say, 1817, p. 160.
Hippa emerita: Ortmann, 1896 (in part), p. 232.
Emerita talpoida: Hay and Shore, 1918, p. 416, pl. 30, fig. 8.—Schmitt, 1935a, p. 216, figs. 74 a, b.—Snodgrass, 1952.

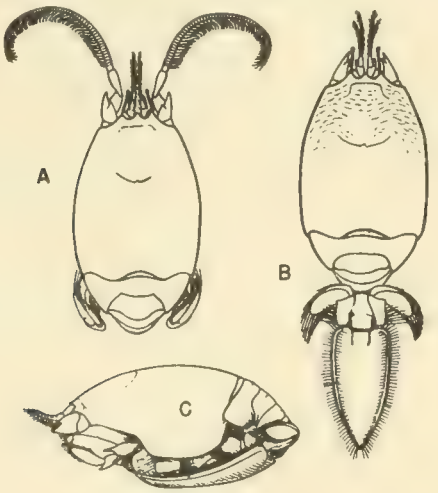

FIGURE 116.—*Emerita talpoida* (Say). A, animal in dorsal view, antennae extended; B, animal in dorsal view, abdomen extended; C, animal in lateral view (after Snodgrass, 1952).

Recognition characters.—Body convex, oval; carapace firm, with overlapping rugosities anteriorly, smoother and polished posteriorly. Anterior margin with a small, blunt rostrum separated by a rounded sinus on each side from a more prominent and acute tooth; an impressed, transverse line behind rostrum, and a deeper, more strongly curved one farther back. Posterolateral margins extending downward to cover bases of legs; anterolateral margins concave and subserrate.

Eyestalks long, slender; cornea minute. Antennules approximately twice length of eyestalks; basal article with a strong, external spine; flagella hairy, forming respiratory tube when approximated. Antennae, normally held concealed beneath third maxillipeds, nearly twice as long as carapace when extended; first peduncular article short, second one largest with outer margin produced into a strong, anteriorly directed spine widely bifid at tip with a deep fissure below; flagellum densely beset laterally with eight rows of fringed setae, outer rows longest. First pair of legs directed forward, articles more or less hairy, and with impressed, interrupted, transverse ciliated lines; dactyl rounded distally, fifth article spinose distally. Second, third, and fourth legs less strong, hairy, tips curved and foliaceous. Fifth legs almost filamentous, entirely concealed beneath abdomen.

Abdomen broadest anteriorly, narrow posteriorly; flexed so that telson and sixth segment lie beneath body. Uropods turned forward, resting along sides of proximal segments. Telson elongate, lanceolate, margined with reflected setae above and inflected ones on edge; base with two short, impressed lines.

Measurements.—Length of carapace: males, 11 mm.; females, 26 mm.

Color.—Uniform pale yellowish brown (Snodgrass, 1952).

Habitat.—Sandy beaches in and below surfline; to 2 fathoms in winter.

Type locality—[East] coast of United States.

Known range.—Harwich, [Barnstable County], Mass., to east coast of Florida; west coast of Florida to Grand Isle, La.; Progreso, Yucatan, Mexico (Schmitt, 1935a).

Remarks.—The general ecology of *Emerita talpoida* as a representative of the specialized sandy-beach fauna has been studied by a number of workers, especially Wharton (1942). The eggs are bright orange when first laid and gradually fade to a translucent dirty gray just before hatching. Wharton gave a figure of the mature sperm cell, and Herrick (1892, pl. 25) gave figures of developmental stages in the egg. Wharton found the breeding season in North Carolina to extend from early June through September, and Fish (1925) found larvae at Woods Hole, Mass., from late July to early September. In Florida, ovigerous females have been found in November. The larval stages were most completely described by

Rees (1959) from rearing experiments in the laboratory. Larval development lasts 28 days and normally encompasses at least six zoeal stages. Rees also described the megalops stage which resembles the adult in shape.

Wharton found megalops in large numbers in sand washed by waves. This stage swims with the abdomen extended, whereas young adults swim with the abdomen flexed. Megalops and young adults were found to be distributed evenly in the wave-washed zone rather than in colonies as are adults. Wharton traced development of the pleopods of females from the truly swimming appendages of the megalops to the uniramous nonswimming pleopods of adults. Adult males lack pleopods.

The average carapace length of young adult females increased from 3 mm. in early summer to 8 mm. the following May, and by August had increased to 18 mm. (maximum, 26 mm.). Wharton thought that females have one reproductive period in summer at an age of about 1 year, then live a short time longer and die at an age of about 1 year and 3 months. Williams (1947), studying size-frequency distributions, thought that they live to be 2 years of age, and Edwards and Irving (1943) stated that at Woods Hole females live 27 months, males 25. Since large females (to 21 mm.) can be taken in winter, the latter estimates are more likely correct, and Wharton's 26-mm. female was probably 2 years old.

Small males appear about the same time as females. Sexually mature at very small sizes (carapace length, 3 mm.) they seek out and attach themselves to year-old females. As many as seven small males were found on a single large female, and Wharton judged that they remain attached for long periods:

> The attachment of the small males to the large females is achieved by various methods. These semiparasitic mates have been found in the gill chambers, clamped between the coxae of the thoracic appendages, attached to egg masses, clamped by means of their telson to the ovigerous hairs of the pleopods, and some seen to roam about on the ventral surface of the larger females. A few males seemed to be attached by means of the spermatophores which are extruded from the basal segment of the fifth leg; however, these may have been merely depositing the spermatophores.

By winter, the males are free living, and by the following June attain a size of about 7 mm. (maximum, 10 mm.). Wharton thought that these die in July after a possible second mating period.

It was estimated that growth of large females from early June to late August may be as much as 0.08 mm. per day. However, both Wharton (1942) and Williams (1947) noticed that there is considerable annual fluctuation in size at the same locality, and Williams further stated that there is considerable variation in size between localities in the same year.

The beautiful adaptations of this species for life in the shifting sand of the surf zone were treated by Wharton, and the anatomical specializations were exhaustively discussed by Snodgrass (1952). Adults can swim by means of the uropods, but they are primarily adapted for burrowing backward into wet sand. This is accomplished by rotating the uropods in unison, throwing sand dorsally, moving the second, third, and fourth legs laterally and posteriorly in unison, and by pushing the first legs alternately laterally and anteriorly. Once the animal is buried, the fringed antennae are allowed to lie on the sand extended anterolaterally to strain the receding water of waves. Stomach contents consist of small particulate matter, but the exact method of transfer of food from the antennae to the mouth is unknown.

Emerita talpoida moves up and down the beach with the tide, following shallow waves toward the water or moving up the beach with deep waves. Jones (1936) compared the habits of *E. emerita* to those of *E. talpoida* and devised a clever method of marking animals with string for the purpose of tracing their movements on the beach.

Edwards and Irving (1943) studied the influence of temperature and season on oxygen consumption in *E. talpoida* at Woods Hole. They found that oxygen consumption of winter animals at 12° C. is about the same as that of the smallest summer animals at 17° C.; consumption of winter animals at 3° C. is about the same as that of summer animals at 13° C. They concluded that *E. talpoida* from the Woods Hole area becomes adjusted to seasonal changes in temperature in such a manner that rate of metabolism in winter is kept at a level comparable to that in summer. This explains why growth is uniform throughout the year, though the animals live in 6 to 12 feet of water in winter rather than in the surf. The method of feeding in winter was not discussed.

Section **Brachyura**

Crabs with abdomen much reduced in size, straight, symmetrical, closely bent under thorax, never used for swimming, and with uropods rarely present, never biramous. Cephalothorax depressed, fused with epistome at sides and nearly always in middle. Antennal scales immovable. Third maxillipeds broad. First pair of legs chelate and nearly always much stronger than other legs.

Subsection **Gymnopleura**

Anterior thoracic sterna broad, posterior thoracic sterna narrow and keellike. Posterior thoracic epimera largely exposed by reduction of branchiostegite. Female openings on coxae. Last pair of legs dorsal in position, normal or reduced in size. Sternal canal present. Thoracic nerve ganglion-chain elongate. Antennary sternum triangular, spout-shaped. Branchiae eight on each side (Bourne, 1922).

Family **Raninidae**

Crabs with carapace remarkably elongate but not covering abdominal terga, first four or five terga lying exposed in dorsal plane of body. Last pair of legs also raised in dorsal plane of body. Antennae and antennules large, not folding into fossettes. Vasa deferentia protruding through bases of fifth pair of legs; oviducts piercing coxa of third pair of legs. Sternum broad anteriorly, narrow or linear posteriorly. A pair of respiratory orifices between tergum of first abdominal segment and coxae of last pair of legs. External maxillipeds completely covering buccal cavity, with palp concealed in repose; exopodite but little longer than ischium. Gills less than nine in number on either side. Hand flat, immovable finger extremely bent allowing movable finger to close against anterior border of hand. (Modified after Alcock, 1896, and Rathbun, 1937.)

Genus ***Ranilia*** H. Milne Edwards, 1837

Rathbun, 1937, p. 17.

Ranilia muricata H. Milne Edwards

Figure 117

Ranilia muricata H. Milne Edwards, 1837, p. 196.— Hay and Shore, 1918, p. 420, pl. 31, fig. 1.—Rathbun, 1937, p. 18, pl. 3, figs. 3–6; pl. 4, figs. 1–4 (rev.).

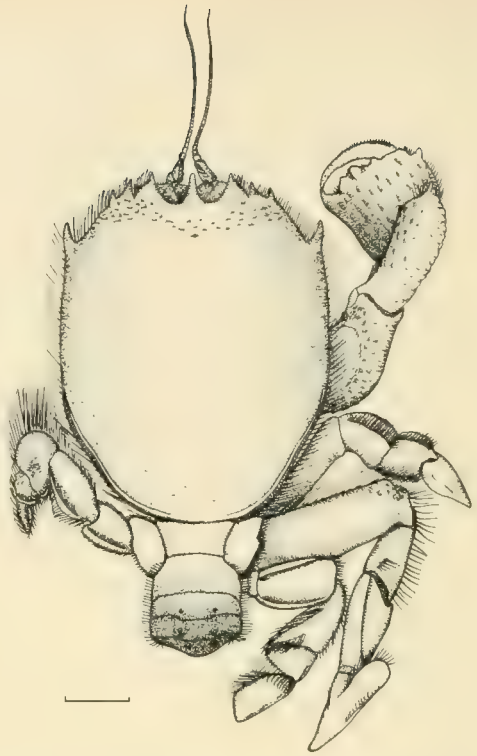

FIGURE 117.—*Ranilia muricata* H. Milne Edwards. Ovigerous female in dorsal view, first to fourth legs of right side shown, only fifth leg of left side shown, 5 mm. indicated.

Recognition characters.—Carapace oval, strongly convex from side to side, slightly so from front to back, smooth posteriorly but with numerous transverse ciliated wrinkles anteriorly. Rostrum slender; anterior border of carapace with four strong spines on each side, innermost overhanging base of orbit, third surmounting external angle of orbit, fourth at external angle of front. Eyestalks strong, about four times as long as rostrum, and capable of being turned back into deep, oblique orbits. Antennules small. Antennae directed forward, slightly longer than eyestalks.

First pair of legs subchelate, stout, flattened distally, squamous-denticulate above, with a strong spine on superodistal margin of merus, carpus, and hand; distal margin of hand perpendicular, toothed; dactyl strong, curved. Second, third, and fourth pairs of legs with flattened, triangular dactyls. Fifth pair of legs elevated, turned forward, fringed with hairs.

Abdomen short and narrow.

Measurements.—Carapace: length, 39 mm.; width, 28 mm.

Color.—Porcelain white with red, vermiculate, transverse lines on cephalothorax, and red dots and blotches on legs. Gibbes, *in* Rathbun (1937) gave the color of dry specimens as purplish mixed with yellow and orange in places, particularly about the articulations and spines, with the latter having white tips, and the chelipeds, walking legs, and abdominal segments with purplish markings.

Habitat.—This species appears to be confined to sand bottoms well offshore. Specimens have been obtained in dredge hauls, and fragments of others taken from fish stomachs off North Carolina. The species has not been found within Beaufort, N.C., harbor, nor along the beaches; 7 to 56 fathoms.

Type locality.—Unknown.

Known range.—Off Cape Lookout, N.C., to northwest Florida; Bahamas; Swan Island in Caribbean Sea.

Remarks.—Though this modern species has no fossil record in North America, the Family Raninidae in this region has a fossil record dating from the Cretaceous (Rathbun, 1935).

Rathbun (1937) reported ovigerous females in April from Florida, and in September from North Carolina.

Subsection **Dromiacea**

Carapace subglobose or subquadrate, frontal region narrow. Last one or two pairs of legs small, subdorsal in position. Abdomen folded under thorax, penultimate segment usually without appendages; five pairs of appendages in female, first pair rudimentary. Lateral thoracic apodemata united in common center, forming a sternal canal. External maxillipeds with merus and ischium subquadrate (Rathbun, 1937).

Family **Dromiidae**

Carapace subglobular, rarely flattened; no *lineae anomuricae* (a pair of longitudinal suture lines on carapace). Sternum of female traversed at least in part by two obliquely longitudinal grooves. External maxillipeds generally operculiform. Legs of moderate size; fourth and fifth pairs short, subdorsal in position, furnished with small hooklike nail or dactyl. Sixth segment of abdomen generally with rudimentary uropods (Schmitt, 1921).

The significance of the obliquely longitudinal sternal grooves on the females of this family has recently been treated by Gordon (1950). She found these to be external evidence of a pair of involuted tubes (variously developed in different species) leading from an external opening at the anterior end of the grooves posteriorly to paired spermathecae enclosed in the endophragmal system.

The North American fossil record for this family dates from the lower Cretaceous of Texas (Rathbun, 1935), though no modern species in the Carolinian fauna possesses a known fossil record.

KEY TO GENERA IN THE CAROLINAS

a. Carapace firm and hard; body covered with short pubescence ..... *Dromidia* (p. 143).

aa. Carapace soft and membranous; body mostly naked ..... *Hypoconcha* (p. 144).

Genus ***Dromidia*** Stimpson, 1858

Rathbun, 1937, p. 32.

Dromidia antillensis Stimpson

Figure 118

Dromidia antillensis Stimpson, 1859, p. 71.—Hay and Shore, 1918, p. 417, pl. 31, fig. 5.—Rathbun, 1937, p. 33, text-fig. 12, pl. 7, figs. 1–3 (rev.).

Recognition characters.—Body and legs covered with thick coat of short pubescence, leaving only parts of fingers exposed. Carapace convex in all directions, longer than broad; frontal region longitudinally grooved along middle; front strongly deflexed, with five small, slender teeth, median three subequal and approximately as long as distance between them at bases, teeth over eyes somewhat shorter but acute. Anterolateral margin of carapace deflected toward corner of buccal area, armed with four or five teeth.

Chelipeds rather thick and heavy; carpus dentate with small teeth at anterior angles; palm shorter than dactyl and armed with three blunt spines on upper margin; fingers curved, with strongly interlocking teeth. Walking legs rather slender; last pair turned forward over back, and much longer than fourth pair; dactyls of fourth and fifth legs hooked, closing against unequal pair of distal spines on propodus.

Measurements.—Carapace of male: length, 32 mm.; width, 31 mm.

FIGURE 118.—*Dromidia antillensis* Stimpson. Male in dorsal view, legs of left side not shown, 10 mm. indicated.

Color.—Quite variable. General ground color dirty yellowish green, olive buff, white, coral-mud gray, orange buff or various shades of red with lighter pubescence; fingers with bases darker than white tips, shades of orange, pink, or red; cornea of eyes gray, hazel, reddish speckled or brown; some specimens with bluish cast on maxillipeds and antennular peduncles. Rathbun (1937) gave great detail on a number of individuals which appeared to vary from light to dark in a harmonious set of colors.

Habitat.—Shore to 170 fathoms.

Type localities.—St. Thomas, V.I., Key Biscayne and Tortugas, Fla.

Known range.—Off Cape Hatteras, N.C., through Gulf of Mexico and West Indies, to State of Bahia, Brazil; Bermuda.

Remarks.—This species is usually found carrying a covering of compound ascidians, sponge, or zoanthoid polyps. The species is primarily southern in distribution, the North Carolina records representing marginal occurrence in a favorable northern locality. Hildebrand (1955) found it common on the Campeche Banks shrimping grounds.

Rathbun (1937) reported ovigerous females from Florida and the West Indies in winter, spring, and summer.

Genus *Hypoconcha* Guérin, 1854

Rathbun, 1937, p. 44.

KEY TO SPECIES IN THE CAROLINAS

a. Anterior margin of carapace without spines *arcuata* (p. 144).

aa. Anterior margin of carapace with several strong spines *sabulosa* (p. 145).

Hypoconcha arcuata Stimpson

Figure 119

Hypoconcha arcuata Stimpson, 1858, p. 226.—Hay and Shore, 1918, p. 418, pl. 31, fig. 2.—Rathbun, 1937, p. 47, pl. 11, figs. 1–4.

Recognition characters.—Body short, broad, flattened, with a thin, parchmentlike covering dorsally, solid and roughly granulate ventrally. Appendages capable of being folded compactly against body. Front margin of carapace nearly semicircular in outline, margin densely ciliated, deeply fissured in middle and with a shallow notch on each side near middle. Ventral surface without ridges, sloping evenly to anterior margin, and with eyes, antennules, antennae, and mouth parts deeply seated in depressions; a narrow fissure in front of eye for lodgment of antennal flagellum; outer posterior margin of orbit fissured. Third maxillipeds completely closing buccal cavity.

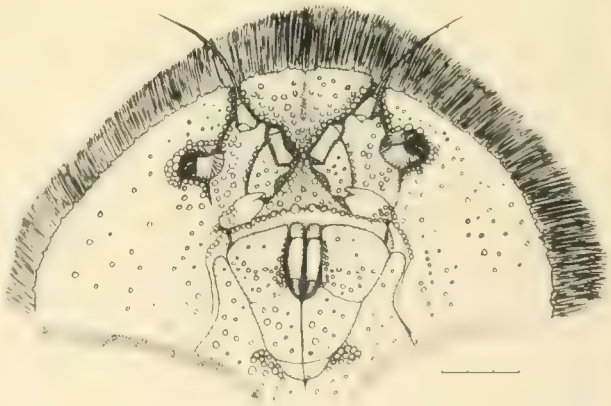

FIGURE 119.—*Hypoconcha arcuata* Stimpson. Anterior portion of animal in ventral view, 3 mm. indicated.

Legs all stout, hairy, and coarsely granulate. First pair chelate; fingers somewhat spatulate and toothed at tip, immovable finger articulated at angle with hand. Second and third legs with sharp, corneous tips; fourth and fifth legs borne on dorsal surface, with penultimate article quite short, and terminal article reduced to a small, curved claw. Abdomen short and flexed so that last two segments lie on thoracic sterna.

Measurements.—Carapace of male: length, 24 mm.; width, 24 mm.

Color.—Gray.

Habitat.—This curious crab has been taken from dredge hauls in Bogue Sound off Morehead City, N.C. It is always found occupying a valve of some lamellibranch shell, preferably a clamshell, which it carries about upon its back after the manner of a hermit crab. By means of the claws on its fourth and fifth pairs of legs, perhaps aided by pressure of its body against the shell, it clings so tightly that removing it from the shell without crushing it is almost impossible. Shallow water to 22 fathoms.

Type localities.—South Carolina sandy shores, and St. Thomas, [V.I.].

Known range.—Off Cape Lookout, N.C., to west Florida; St. Thomas, V.I.; Surinam to State of Espirito Santo, Brazil.

Hypoconcha sabulosa (Herbst)

Figure 120

Cancer sabulosa Herbst, 1799, p. 57, pl. 48, figs. 2–3.
Hypoconcha sabulosa: Hay and Shore, 1918, p. 418, pl. 31, fig. 3.—Rathbun, 1937, p. 44, pl. 8, figs. 3–4, pl. 9, figs. 1–5 (rev.).

Recognition characters.—Body short, broad, flattened, with front and lateral margin expanded, with thin parchmentlike covering dorsally, solid with surface nodulose, granulate, and marked by several strong ridges ventrally. Carapace in old individuals pubescent above; margin densely hairy, and armed anteriorly with four curved spines with sharp tips pointing obliquely downward followed by a few other smaller spines; front between median pair of spines subtruncate or sloping slightly backward toward short, narrow, median fissure. Antennal fossae limited in front by a pair of strong, oblique ridges arising between two of spines of anterior border, meeting each other in midline in front of epistome; epistome with posterior border raised into a prominent ridge continuing on either side across front and some distance along sides of buccal area. Basal articles of antennae tuberculate; proximal article with a strong inwardly directed tooth, distal article with a tooth on each side of base of flagellum. Fissure in outer margin of orbit prominent owing to development of a strong tubercle on either side.

FIGURE 120.—*Hypoconcha sabulosa* (Herbst). Anterior portion of animal in ventral view, detail of right side shown, 5 mm. indicated.

Carpal article of first pair of legs with several dentate tubercles; hand covered with more or less pointed tubercles. Other legs and abdomen much as in *H. arcuata.*

Measurements.—Carapace of female: length, 22 mm.; width, 22 mm.

Color.—Gray; or, as described by Schmitt in Rathbun (1937), coral sand above with whitish-gray hairs, ground color beneath, red; rounded bosses on legs and subfrontal region reddish brown; eyes black or reddish brown; eggs orange.

Habitat.—A few feet to 49 fathoms.

Type locality.—Listed as "Africa" (probably an error).

Known range.—Off Cape Hatteras, N.C., to Sabine, Tex.; Jamaica.

Remarks.—This species has been found in Beaufort, N.C., harbor, and, though it apparently has habits similar to those of *H. arcuata*, it is much the rarer of the two species. Rathbun (1937) listed ovigerous females in June from Florida and in October from North Carolina.

Family **Homolidae**

Crabs with carapace rectangular, ovoid, or urn-shaped, longer than broad. Eyes incompletely sheltered by orbits when retracted, terminal joint of eyestalk either longer or shorter than slender basal joint. External maxillipeds pediform, subpediform, or suboperculiform. Sternum of female without longitudinal grooves. Gills 8, 10, 13, or 14 on each side (Rathbun, 1937, modified after Gordon, 1950; Hemming, 1958c).

Genus ***Homola*** Leach, 1815

Rathbun, 1937, p. 62.—Hemming, 1958c.

Homola barbata (Fabricius)

Figure 121

Cancer barbatus Fabricius, 1793, p. 460.
Homola barbata: Hay and Shore, 1918, p. 419, pl. 30, fig. 10.
Thelxiope barbata: Rathbun, 1937, p. 63, text-fig. 16, pl. 15, figs. 1–2 (rev.).

FIGURE 121.—*Homola barbata* (Fabricius). Animal in dorsal view (after Smith, 1887).

Recognition characters.—Carapace about one-fourth longer than wide with surface granulate, spinulose, and sparsely setose; *linea anomurica* distinct and dorsal; sides nearly straight, only slightly convergent posteriorly, and extending almost vertically downward from a spiny ridge running backward from behind a strong spine situated at extremities of suture separating gastric and hepatic regions. Rostrum small, bifurcate at tip; a spine on each side at base of rostrum, one at outer orbital angle, a transverse row of two behind rostrum, behind these a transverse row of eight, and farther back a small median spine. Anterolateral parts below and behind orbits with small spines. Eyestalks long, slender at base, and abruptly enlarged below cornea.

Chelipeds of moderate size, surface granulate and hairy; merus and carpus with rows of spines. Walking legs with flattened articles, long, hairy, and spinulose along margins. Second segment of abdomen with a large, median, conical tooth.

Measurements.—Carapace including rostrum: male, length, 30 mm., width at base of lateral spines, 22 mm., posterior width, 16 mm.; female, length, 33 mm., width at spines, 25 mm., posterior width, 20 mm.

Color.—"Body covered with tawny or yellowish-brown or reddish-brown hair; spines red or partly red" (Rathbun, 1937).

Habitat.—Thirty to 373 fathoms.

Type locality.—Bay of Naples.

Known range.—Off southeastern Massachusetts to Caribbean Sea; eastern Atlantic Ocean from Portugal and Azores to Madeira Islands; Mediterranean Sea; South Africa.

Remarks.—This essentially deep-water species has been reported in 63 fathoms off North Carolina. Ovigerous females have been reported in October off Delaware Bay (Rathbun, 1937), and are known off North Carolina and Florida in June and July.

Gordon (1950) discussed the anatomical structure of the spermathecae of females and copulatory apparatus of males in the genus *Homola*, and remarked upon the evolutionary sequence shown by these structures in the Dromiacea.

Subsection **Oxystomata**

Epistome reduced or absent. Efferent branchial channels terminating at middle of buccal area, buccal cavern produced forward and generally elongate-triangular in shape, efferent channels enclosed by an elongate lamellar process of exopods of first maxillipeds. Afferent branchial openings either in front of bases of chelipeds, or at sides of endostome. Gills six to nine on each side. Antennules folding either longitudinally or obliquely, rarely transversely. Male genital ducts protruding through bases of fifth legs or through

fifth thoracic sternum nearby. (Modified after Alcock, 1896, *in* Rathbun, 1937.)

Family **Leucosiidae**

Crabs having carapace circular, oval, or polygonal. Eyes and orbits small, front narrow but wider than orbit. Antennules folding more or less obliquely. Antennae small. External maxillipeds completely enclosing buccal cavity, except often a small crevice in front. Afferent branchial channels occupying sides of endostome on either side of deep, median, endostomal groove serving as an efferent branchial channel. Afferent channels covered by exognaths of external (third) maxillipeds, efferent channels by a pair of lamellar processes of first maxillipeds. Chelipeds symmetrical. Abdomen hidden beneath thorax, commonly with third to sixth abdominal terga fused, sixth sometimes free. Vasa deferentia opening on fifth thoracic sternum near bases of last pair of legs. (Modified after Alcock, 1896, *in* Rathbun, 1937.)

KEY TO GENERA AND SOME SPECIES IN THE CAROLINAS

a. Carapace polygonal, uneven, nodular, or eroded
Subfamily Ebaliinae (p. 147).
b. Posterior portion of carapace without deep cavities
Ebalia cariosa (p. 147).
bb. Posterior portion of carapace with a deep rounded cavity on each side ..... *Speloeophorus* (p. 148).
aa. Carapace ovoid or globular, and smooth or granular
Subfamily Philyrinae (p. 150).
b. Fingers opening in horizontal plane
Persephona punctata aquilonaris (p. 150).
bb. Fingers opening in vertical plane
Iliacantha (p. 150).

Subfamily **Ebaliinae**

Surface of carapace uneven. Chelipeds of moderate length; fingers not very thin and elongate, dactyl moving in an oblique plane. Anterior margin of buccal cavity arcuate, middle part in front of level of anterior pterygostomian region. Epistome and infraorbital lobe well developed. Pterygostomian margin extending either slightly or distinctly forward, terminating in an indentation. Merus of external maxillipeds half or more than half length of ischium measured along inner border. First abdominal segment in female often under carapace (Rathbun, 1937).

Genus *Ebalia* Leach, [1817]

Rathbun, 1937, p. 123.—Hemming, 1958b, p. 15.

Ebalia cariosa (Stimpson)

Figure 122

Lithadia cariosa Stimpson, 1860a, p. 238.—Hay and Shore, 1918, p. 424, pl. 32, fig. 6.

Ebalia cariosa: Rathbun, 1937, p. 125, pl. 35, figs. 6–7 (rev.).

FIGURE 122.—*Ebalia cariosa* (Stimpson). Animal in dorsal view, legs of left side not shown, 3 mm. indicated.

Recognition characters. — Carapace convex, roughly pentagonal; anterior angle truncate, lateral angles obtuse; surface uneven and covered everywhere, including other parts of body and legs, with beadlike granules, larger posteriorly and ventrally. Front narrow, upturned, and broadly notched, connected with middle protuberances by a median ridge traversing gastric region; ridge flanked on each side by a sinuous, deep, broad excavation of darker color than protuberant parts. Anterolateral margin of hepatic region sinuous, hepatic region slightly prominent, delimited posteriorly by an impressed line. Pterygostomian region with a large downward-pointing tooth, hardly visible in dorsal view. Posterolateral margin with a broad tooth, separated from bilobate intestinal region by a deep sinus; cardiac and inner lobules of branchial region strongly protuberant, separated from thick intestinal lobes by a deep narrow sulcus.

Chelipeds stout, a little longer than width of carapace, joints angular; merus as broad as hand, outer margin convex and a little irregular; hands rather small, tapering to rather slender fingers. Walking legs cylindrical. Abdomen of male narrow, triangular, with a backward projecting spine at proximal end of penultimate segment. Abdomen of female with penultimate segment very large, nearly circular.

Measurements.—Carapace: length of male, 12 mm., width, 13 mm.; female, length, 13 mm., width, 15 mm.

Color.—Light gray or buff, female occasionally with two or three small red spots on abdomen; other specimens may be pale red (Rathbun, 1937).

Habitat.—Below low-tide mark to 25 fathoms.

Type locality.—Beaufort, N.C.

Known range.—Bogue Sound near Beaufort, N.C., to west Florida; Jamaica; northeastern South America to Rio de Janeiro, Brazil.

Remarks.—This species is occasionally found in channels in the Beaufort, N.C., harbor. The species feigns death when brought on deck in a dredge haul, and, thus, closely resembles the pebbles and pieces of shell among which it appears to live. Ovigerous females are found at this locality throughout the summer.

Genus ***Speloeophorus*** Milne Edwards, 1865

Rathbun, 1937, p. 141.

KEY TO SPECIES IN THE CAROLINAS

a. Lateral portions of carapace tumid, not expanded into wings; deep cavity of carapace with only two openings, not visible dorsally ..... *nodosus* (p. 149).

aa. Lateral portions of carapace expanded into broad, flattened wings; deep cavity of carapace with four openings, two visible dorsally ..... *pontifer* (p. 149).

Speloeophorus nodosus (Bell)

Figures 123–124

Oreophorus nodosus Bell, 1855, p. 307, pl. 33, fig. 8.

Speloeophorus nodosus: Hay and Shore, 1918, p. 425, pl. 32, fig. 5.—Rathbun, 1937, p. 142, pl. 40, figs. 1–5.

Recognition characters.—Carapace convex, roughly pentagonal or hexagonal, broader than long, posterolateral angles rounded; surface nodose, evenly and thickly covered everywhere with crowded, rounded granules. Front thick, bilobed, upturned; a prominent broad ridge extending backward from front to cardiac region. Hepatic region to each side with a low hump, behind this,

FIGURE 123.—*Speloeophorus nodosus* (Bell). Animal in dorsal view, legs of left side not shown, 3 mm. indicated.

FIGURE 124.—*Speloeophorus nodosus* (Bell). Animal in posterior view, 3 mm. indicated.

at side of gastric region, a much larger hump, and still farther back, near posterior border, another of nearly equal size; posterior humps overhanging and largely containing a deep cavity with two openings invisible in dorsal view. Subhepatic region with a nodose prominence near front, and farther back two others of smaller size.

Chelipeds short, stout, coarsely granulate, crested along outer margin; merus with large distal and small proximal lobe; fingers thin, flat, grooved. Walking legs crested, crests dentate or narrowly lobed.

Measurements.—Carapace: length of male, 12 mm., width, 15 mm.; female, length, 17 mm., width, 21 mm.

Variations.—Carapace of males much more uneven than that of females.

Color.—Pink with a few purplish spots on carapace and rusty-brown marks on legs. Rathbun (1937) described this species as looking like a dead piece of coral overgrown with purplish and greenish algae, with patches of red ones; chelae with natural greenish cast; reticulations around whitish areas of green hue; fingers dull white with articulations pink; legs dirty white with greenish, reddish, and whitish spots; eyes not distinguishable from rest of body; underparts dirty white, abdomen greenish.

Habitat.—One and one-half to 10 fathoms.

Type locality.—Unknown.

Known range.—Off Morehead City, N.C., to southern Florida; West Indies.

Remarks.—This species is rare in the northern part of its range and was most recently reported by Pearse and Williams (1951) from reefs off Beaufort Inlet, N.C. The species readily plays dead when brought on deck.

Speloeophorus pontifer (Stimpson)

Figures 125–126

Lithadia pontifera Stimpson, 1871b, p. 115.

Speloeophorus pontifera: Hay and Shore, 1918, p. 425, pl. 32, fig. 5.

Speloeophorus pontifer: Rathbun, 1937, p. 144, pl. 39, figs. 1–3 (rev.).

Recognition characters.—Carapace angular, roughly trefoil shaped, from one-third to one-sixth wider than long; surface granulate, uneven. Lateral margin of each side extended into a broad wing projecting over bases of legs; anterolateral margins concave, with notch near middle; posterolateral margins broad, with a deep rounded cavity to each side of intestinal region, extending toward and almost to much smaller pit on dorsal surface at side of cardiac region, a narrow suture connecting cavity and pit of each side. Front narrow, produced, upturned, and with a deep median sinus. Orbits small. A middorsal ridge extending from front almost to posterior margin, ridge interrupted in middle of carapace; branchial region on each side with a prominent elevation more or less divided into two parts, one connected by a ridge to anterior angle of lateral wing, other similarly connected to posterior angle. Hepatic region small, slightly elevated; pterygostomian region prominent, with conical downward-pointing eminence visible from above.

Chelipeds of moderate size, somewhat crested; merus with two large triangular teeth on outer margin; fingers slender and curved. Walking legs granulate and tuberculate.

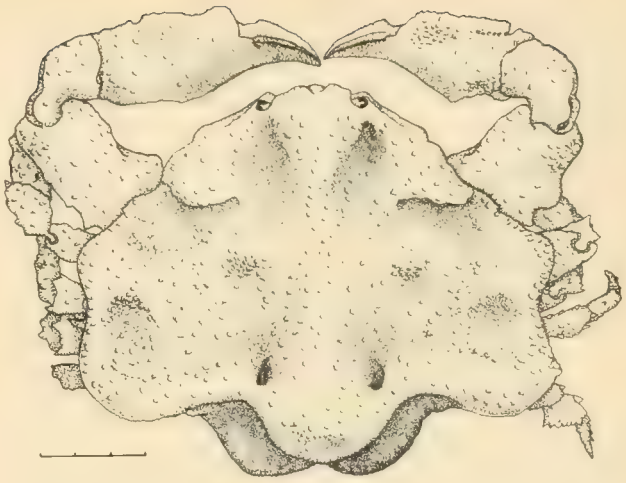

FIGURE 125.—*Speloeophorus pontifer* (Stimpson). Female in dorsal view, 3 mm. indicated.

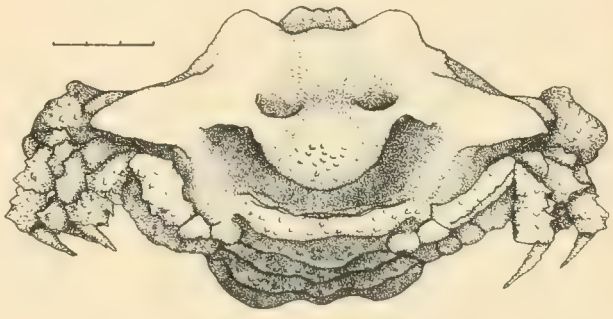

FIGURE 126.—*Speloeophorus pontifer* (Stimpson). Female in posterior view, 3 mm. indicated.

Abdomen tuberculate; segments three to five only partially fused; sixth segment with a sharp, backward pointing, proximal spine.

Measurements.—Carapace: length of male, 6 mm., width, 8 mm.; female, length, 10 mm., width, 13 mm.

Variations.—This small species apparently attains a width of about 15 mm., and is extremely variable. The ridges and elevations of the dorsal surface may be sharp and conspicuous or low and rounded; the lateral angles of the lateral wings of the carapace may be produced or rounded off. The female is not so wide in proportion to length as the male, and is somewhat tumid on the outer posterior part of the lateral wings.

Color.—Pale red in middle, remainder white (von Martens *in* Rathbun, 1937.)

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Habitat.—Low tide to 125 fathoms.

Type locality.—Barbados.

Known range.—Off Beaufort, N.C., to west Florida; West Indies to Barbados.

Subfamily **Philyrinae**

Carapace almost hemispherical, surface only slightly uneven. So-called frontal teeth often being well-developed inner-orbital angles. A median frontal tooth often present. Infraorbital lobe seldom well developed, roof of efferent branchial channel usually reaching same level. Epistome usually reduced. Margins of mouth and pterygostomian region in same transverse plane. Merus of external maxillipeds half or more than half length of ischium measured along inner border. First abdominal segment in female often under carapace (Rathbun, 1937).

Genus ***Persephona*** Leach, 1817

Rathbun, 1937, p. 151.—Hemming, 1958b, p. 18.

Persephona punctata aquilonaris Rathbun. Purse crab

Figure 127

Persephona punctata Stimpson, 1859 (in part), p. 70. -Hay and Shore, 1918 (in part), p. 423, pl. 32, fig. 9.

Persephona punctata aquilonaris Rathbun, 1937, p. 154, pl. 42, figs. 6–7 (rev.).

Recognition characters.—Carapace globular, thickly strewn dorsally and laterally with granules of various sizes, and with three sharp, recurved spines, one at each end of posterior margin and one median just above posterior margin. Front narrow, broadly bidentate, produced and elevated, and with dentiform angles of branchial channels projecting slightly beyond it. Anterior and lateral regions bounded externally by a row of beadlike granules broken anteriorly by a single tubercle of larger size, and posteriorly extending to a point nearly opposite termination of posterior margin.

Chelipeds subcylindrical in adult male, approximately 1.5 times as long as carapace; merus with many large tubercles; carpus and chela nearly smooth except on margins; chela somewhat flat and dilated; fingers weak.

Measurements.—Male: length of carapace to tip of posterior spine, 48 mm.; to base of spine, 45 mm.; width, 42 mm.

Color.—Gray to grayish brown, with darker brownish irregular spots or marmorations; granules white or tinged with red.

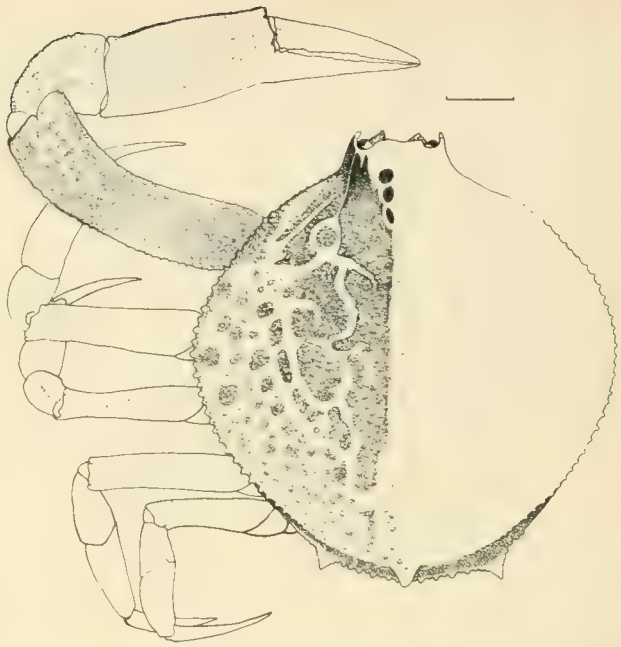

FIGURE 127.—*Persephona punctata aquilonaris* Rathbun. Animal in dorsal view, detail of left side shown, 5 mm. indicated.

Habitat.—This crab is sometimes taken in otter trawls but usually by dredging in shelly mud in relatively shallow water in the ocean; 2 to 30 fathoms.

Type locality.—St. Augustine, Fla.

Known range.—New Jersey to Campeche, Mexico (Hildebrand, 1954, in part).

Remarks.—The species is fairly abundant in colonies. The purselike receptacle formed by the enormously enlarged penultimate segment of the abdomen in the female may be found filled with eggs at almost any time during spring and summer.

Genus ***Iliacantha*** Stimpson, 1871

Rathbun, 1937, p. 183.

KEY TO SPECIES IN THE CAROLINAS

a. Fingers longer than palm of hand—*subglobosa* (p. 150).

aa. Fingers about half as long as palm of hand *intermedia* (p. 151).

Iliacantha subglobosa Stimpson

Figure 128

Iliacantha subglobosa Stimpson, 1871a, p. 155.—Hay and Shore, 1918, p. 424, pl. 32, fig. 2.—Rathbun, 1937, p. 185, pl. 53, figs. 1–2 (rev.).

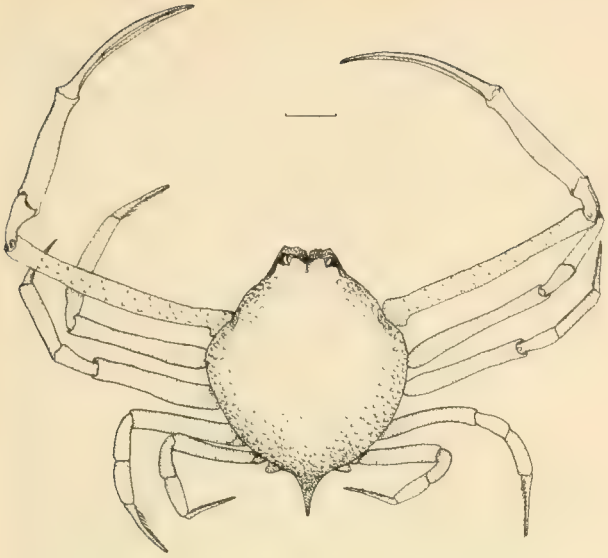

FIGURE 128.—*Iliacantha subglobosa* Stimpson. Female in dorsal view, 5 mm. indicated.

Recognition characters.—Carapace orbicular, smoothly and evenly convex, finely granulate, unarmed except posterior border with three spines; lateral spines subtriangular, blunt; median one higher, longer, conical, and curved upward. Front deeply grooved above, broadly notched anteriorly and with spiniform angles of branchial channels extending beyond it. Margin of carapace distinct, somewhat acute on hepatic region and anterior portion of branchial region, indistinct beyond; hepatic region swollen; intestinal region slightly protuberant above base of median spine.

Chelipeds 2.5 times as long as carapace, excluding spine, finely granulate; merus more sharply granulate than carpus and hand; fingers slender, longer than palm, armed with needlelike teeth. Walking legs slender, smooth; merus as long as three terminal articles; dactyls grooved, and with two fringes of hair on upper and posterior surfaces. Male abdomen gradually tapering from fifth to seventh segment.

Measurements.—Male: carapace length, 21 mm., width, 16 mm.; chela length, 22 mm.; fingers, 13 mm.

Habitat.—Fifteen to 215 fathoms.

Type localities.—Three stations in Florida reefs, 40–80 fathoms.

Known range.—Off Cape Hatteras, N.C., to northwest Florida; through West Indies to Barbados.

Remarks.—Ovigerous females have been taken in June from the Gulf of Mexico.

Iliacantha intermedia Miers

Figure 129

Iliacantha intermedia Miers, 1886, p. 302, pl. 26, figs. 3, 3a.—Hay and Shore, 1918, p. 424, pl. 32, fig. 3.—Rathbun, 1937, p. 186, pl. 54, figs. 1–2 (rev.).

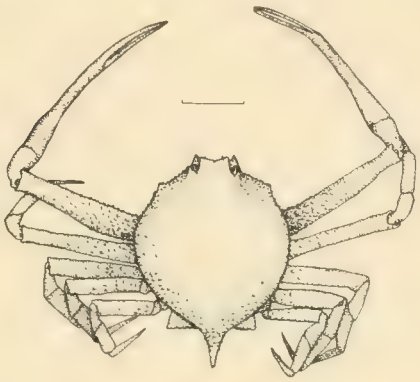

FIGURE 129.—*Iliacantha intermedia* Miers. Male in dorsal view, 5 mm. indicated.

Recognition characters.—Similar to *I. subglobosa*, but carapace more coarsely granulate; posterior spines shorter, flattened, triangular, connected by prominent line of granules. Front deeply grooved above, broadly notched anteriorly, and with spiniform angles of branchial channels extending beyond it. Margin of carapace distinctly granulate; intestinal region not protuberant above median spine.

Chelipeds slender, nearly as long as carapace; merus cylindrical and granulate with coarser granulations proximally; hand smooth, somewhat inflated proximally but tapering to slender fingers; fingers about half as long as palm, incurved at tip, and denticulate on opposed margins. Male abdomen widened at convex-sided sixth segment.

Measurements.—Male: carapace length, 16 mm., width, 12 mm.; chela, length, 13 mm.; fingers, 4 mm. Female: carapace length, 27 mm., width, 21 mm.

Color.—Gray without markings of any kind.

Habitat.—Five and one-half to 180 fathoms.

Type locality.—Bahia, Brazil.

Known range.—Off Beaufort, N.C., to northwest Florida; St. Thomas, V.I.; Venezuela; Bahia, Brazil.

Remarks.—The young of this species and *Persephona punctata aquilonaris* have a close resemblance.

Family Calappidae

Oxystomata of normal crablike form with abdomen hidden beneath thorax. Antennae small. Afferent openings of gill chambers in front of chelipeds. Outer maxillipeds not completely closing buccal cavity. Male openings coxal on fifth pair of legs.

Calappid species are known from the Cretaceous to the present in North America (Rathbun, 1935).

KEY TO GENERA AND ONE SPECIES IN THE CAROLINAS

a. Posterolateral region of carapace expanded and dentate ..... *Calappa* (p. 152).
aa. Posterolateral region of carapace not expanded.
  b. Merus bispinous on distal outer surface with lower spine strong and greatly extended laterally ..... *Acanthocarpus alexandri* (p. 156).
  bb. Merus not bispinous or distal outer surface.
    c. Carapace considerably broader than long, regularly convex above ..... *Hepatus* (p. 157).
    cc. Carapace nearly as long as broad, dorsal surface uneven ..... *Osachila* (p. 159).

Subfamily Calappinae

Merus of external maxillipeds almost never elongate and acute, never concealing palp in repose. Legs adapted for walking (Alcock *in* Rathbun, 1937).

Genus *Calappa* Weber, 1795

Rathbun, 1937, p. 197.

KEY TO SPECIES IN THE CAROLINAS

a. Carapace widest behind middle; proximal tooth on lower edge of hand with margin pointed or angled.
  b. Carapace smoothly granulate.
    c. Carapace often with a horizontal tooth or spine at either end of posterior margin; smooth area on lower half of palm on cheliped narrow proximally, widening and continued obliquely upward distally ..... *sulcata* (p. 155).
    cc. Carapace without a horizontal tooth or spine at either end of posterior margin; smooth area on lower half of palm on cheliped concave, not directed obliquely upward distally.
      d. Male with basal width of fifth abdominal segment twice median length; female with a few granulations near lateral border of fourth abdominal segment ..... *flammea* (p. 152).
      dd. Male with basal width of fifth abdominal segment less than twice median length; female with no granulations near lateral border of fourth abdominal segment ..... *ocellata* (p. 153).
  bb. Carapace covered with rough protuberances, and granulate ..... *angusta* (p. 154).
aa. Carapace widest in front of middle; proximal tooth on lower edge of hand with margin not pointed or angled ..... *angusta* (young) (p. 154).

Calappa flammea (Herbst)

Figures 130–131

Cancer flammeus Herbst, 1794, p. 161, pl. 40, fig. 2.
Calappa flammea: Hay and Shore, 1918, p. 421, pl. 31, fig. 8.—Holthuis, 1958, p. 148, figs. 28–35 (rev.).

FIGURE 130.—*Calappa flammea* (Herbst). Female from Tortugas, Florida, in dorsal view, approximately × 0.66 (after Holthuis, 1958).

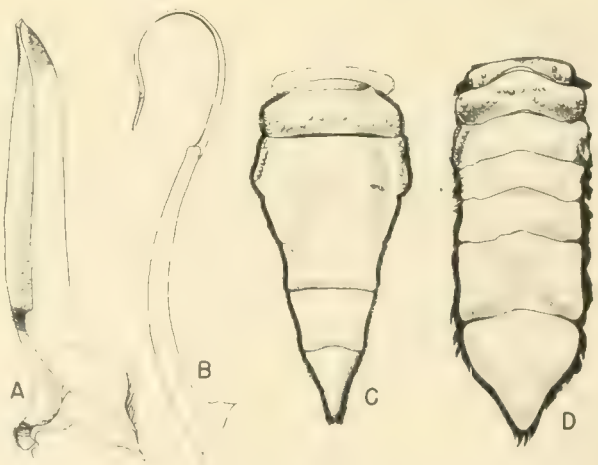

FIGURE 131.—*Calappa flammea* (Herbst). A, male first pleopod in ventral view, × 3; B, male second pleopod in dorsal (anterior) view, × 3; C, abdomen of male, approximately × 0.8; D, abdomen of female, approximately × 0.8; A–C from Tortugas, D from Bahama Islands (after Holthuis, 1958).

Recognition characters.—Carapace 1.14 to 1.42 times broader than long, varying from smaller to larger ratio with increasing size; surface granular, less conspicuously so in posterior half, tuberculate anteriorly, becoming obsolescent in adults; branchiocardiac grooves distinct. Front deeply notched anteriorly, projecting somewhat beyond orbits; anterolateral borders together forming a semicircle in younger specimens, less strongly arched in adults. Posterolateral winglike expansions of carapace distinct, consisting of five broad teeth with beaded edges, second and third with sharp but not pointed apices, fifth tooth with notch on inner basal part.

Chelipeds with outer surface of palm divided into three horizontal zones: a lower one with many large granules; a second zone, slightly sunken, with no large granules but with scattered small ones, more in males than females; a third zone occupying whole upper half of outer surface of palm, separated from second zone by a row of small granules, bearing many small granules, and some large low granular tubercles, more densely granulated than second zone in females, same in both in males. Upper margin of large hand with about seven teeth, six on small hand; proximal teeth broad, low, and bifurcated. Palm with strong tooth on outer lower surface near carpus, apex of tooth approximately rectangular with a sharp tip. Fingers of crushing hand somewhat stouter than on cutting hand, and with prominent projecting lobule near base of each. Merus with strong four-toothed crest parallel with outer distal border.

Male with abdomen narrow; third to fifth segments fused, fifth segment with basal width twice median length, sixth with width greater than length, seventh with length about 1.5 times width. Female with a few granulations near lateral border of fourth segment; length of seventh segment equal to or slightly greater than width.

Measurements.—Carapace: male, length, 99 mm., width, 136 mm.; female, length, 106 mm., width, 135 mm.

Color.—Ground color of carapace gray behind, shading to drab mottled with white over greater portion; reddish blue on outer surface of chelipeds becoming almost white on lower half of palm and on fingers; inner surface of chelipeds, pterygostomian regions, anterior surface of first walking legs, and a small part of second walking legs reddish hued. Carapace with color pattern variable, purplish brown in interlacing bands on anterior half, obliquely longitudinal stripes on posterior half becoming lighter posteriorly. Merus, carpus, and proximal upper portion of palm striped with purplish brown, two distinct round spots of same color in middle of palm; upper half of palm with spots and patches of sulphur yellow on teeth and tubercles and same color mixed with ground color of merus, carpus, and part of carapace; two or three orange spots on hands near base of dactyls and spots of same near articulation of palm and carpus. Third to fifth legs, and underparts whitish. (Adapted from R. L. Barney *in* Rathbun, 1937.)

Habitat.—This strikingly colored crab does not often occur within the harbor at Beaufort, N.C., but is often brought up from a few fathoms outside the inlet. Those obtained inside are usually small. Hildebrand (1955) listed the species as common from 6 to 16 fathoms on the Campeche Banks. The species may spend much time buried in sand (Pearse, Humm, and Wharton, 1942).

Habitat.—Surface to 40 fathoms, rarely to 125 fathoms.

Type locality.—America.

Known range.—Cape Hatteras, N.C., to Florida Keys; Gulf coast of United States and Mexico; Bahamas; Bermuda.

Remarks.—This species has a fossil record in North America dating from the Oligocene (Rathbun, 1930b).

The breeding range of the species extends as far northward as Cape Hatteras, but in the larval stages it often drifts as far to the north as southern New England. Some of these larvae are supposed now and then to survive a mild winter and develop by the next summer into the small specimens which have at rare intervals been taken on the coast of Massachusetts and Rhode Island. Some of the larval stages have been figured by Lebour (1944). Smith (1880b) gave a description of the megalops stage of this species.

Calappa ocellata Holthuis

Figures 132–133

Holthuis, 1958, p. 158, figs. 36–40 (rev.).

Recognition characters.—Carapace slightly narrower than in *C. flammea*, having width to

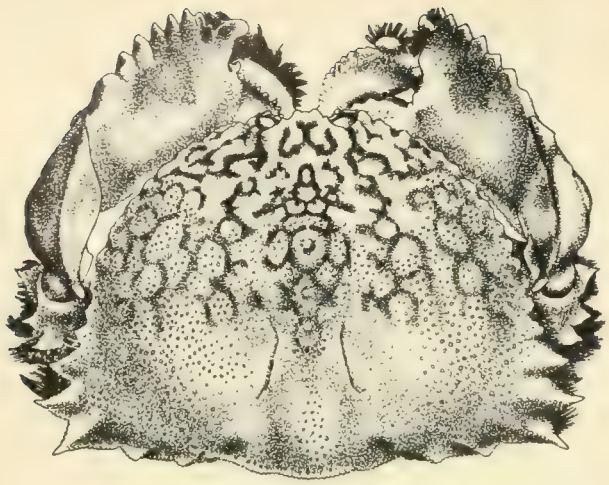

FIGURE 132.—*Calappa ocellata* Holthuis. Male from Curaçao in dorsal view, approximately natural size (after Holthuis, 1958).

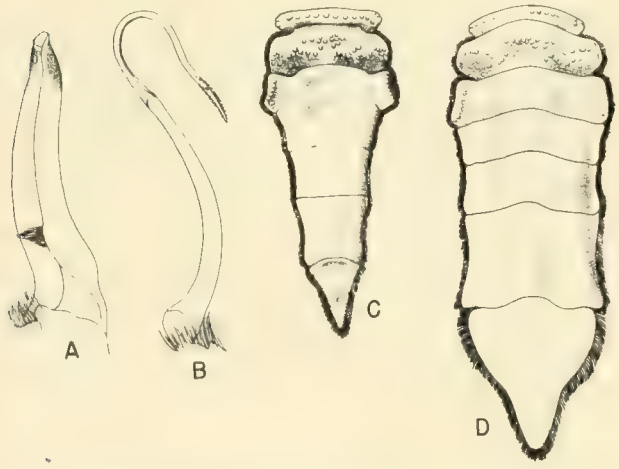

FIGURE 133.—*Calappa ocellata* Holthuis. A, male first pleopod in ventral view, × 3; B, male second pleopod in dorsal (anterior) view, × 3; C, abdomen of male, approximately × 0.8; D, abdomen of female, approximately × 0.8; A–D from Dutch West Indies (after Holthuis, 1958).

length ratio of 1.15 to 1.40, varying from smaller to larger ratio with increasing size; granulations much coarser than in *C. flammea*, granules larger, fewer, and more widely separated. Posterolateral winglike projections distinctly set off from anterolateral margin, teeth with slender pointed tips, more slender than in *C. flammea*, notch in basal part of fifth tooth inconspicuous.

Chelipeds similar to *C. flammea*, though second and third zones of outer palm nearly alike in both males and females. Upper margin with teeth narrower proximally than in *C. flammea*, and with bifurcation indistinct or absent. Palm with strong tooth on outer lower surface near carpus, apex sharply pointed with an acute tip. Teeth on crest of merus more sharply pointed than in *C. flammea*.

Male with abdomen narrower than in *C. flammea;* third to fifth segments fused, fifth segment with basal width less than twice median length, sixth with width equal to or less than length, seventh more slender than in *C. flammea*. Females with no granules near lateral border of fourth segment; length of seventh segment distinctly greater than width.

Measurements.—Male holotype: length of carapace, 83 mm.; width, 114 mm.

Color.—In preserved specimens, anterior half of carapace red with numerous white, often ocellated, spots and a few white streaks, the whole forming a reticulate pattern of red. Pattern more compact and complete than in *C. flammea*, extending over full width of anterior half of carapace, absent in posterior half showing only a few distinct spots between teeth of posterolateral wings, and two red spots before posterior margin above bases of last legs. Chelipeds with one or two red spots near articulation of dactyls; red between teeth of upper margin; inside of chelipeds reddish (Holthuis, 1958).

Habitat.—Shallow water to 14 fathoms.

Type locality.—Klein Bonaire, Dutch West Indies.

Known range.—Cape Hatteras, N.C., to State of Pernambuco, Brazil; Bermuda.

Remarks.—This species is less common than *C. flammea* from Tortugas northward (Holthuis, 1958).

Calappa angusta Milne Edwards

Figure 134

Calappa angusta Milne Edwards, 1880, p. 18.—Hay and Shore, 1918, p. 421, pl. 31, fig. 7.—Rathbun, 1937, p. 210, pl. 64, figs. 1–6 (rev.).

Recognition characters.—Carapace eight-ninths as long as wide; anterolateral margins finely granulate with larger granules at intervals; surface covered with protuberances, granulate between. Tooth at posterolateral angle of winglike extension of carapace largest, preceded anteriorly by four teeth gradually diminishing in size, and followed posteriorly by one small and one or two

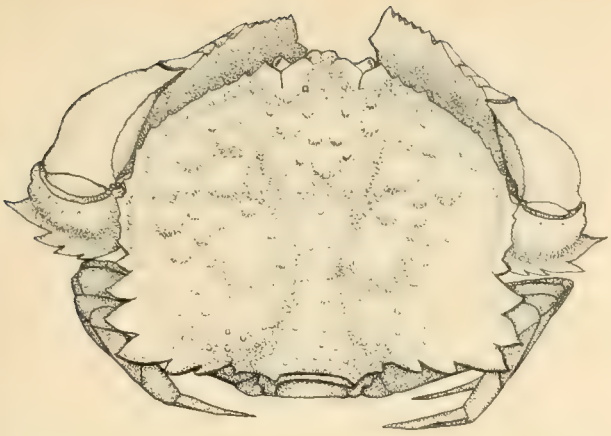

FIGURE 134.—*Calappa angusta* Milne Edwards. Animal from North Carolina in dorsal view, approximately × 1.8.

extremely small teeth. Orbit completely separated from antennular cavity.

Chelipeds with outer surface of palm divided into three zones as in preceding species; upper margin with six to eight teeth. Abdomen with sixth segment subquadrate; seventh segment subtriangular, slightly longer than wide.

Measurements.—Carapace: male, length, 28 mm., width, 32 mm.; female, length, 23 mm., width, 28 mm.

Variations.—Posterior part narrower than middle of carapace in juveniles, wider than middle in adults.

Color.—Ground color buff to buff yellow; high spots or lumps on carapace and chelipeds red. Marginal spines of carapace, crest of chela and lumps on crest drab. Hairs of carapace, especially those of hind margin, light olive yellow; those of walking legs light citrous yellow. Merus of chelipeds practically colorless. Under parts whitish, pterygostomian region and maxillipeds suffused with pale purple (Schmitt *in* Rathbun, 1937).

Habitat.—More abundant in the Gulf Stream than in adjacent inshore waters; 7.5 to 115 fathoms, rarely deeper.

Type locality.—Barbados.

Known range.—Off Cape Lookout, N.C., through eastern Gulf of Mexico, to Grenada.

Remarks.—Ovigerous females have been taken from southern Florida in March.

Calappa sulcata Rathbun

Figures 135–136

Calappa sulcata Rathbun, 1898, p. 289, pl. 9, figs. 3–4.—Hay and Shore, 1918, p. 422, pl. 31, fig. 6.—Holthuis, 1958, p. 179, figs. 51–54 (rev.).

Recognition characters.—Carapace somewhat wider than long, covered with uniform granulations giving appearance of being smooth. Anterolateral margins crenulate and granulate, grading into inconspicuous anterolateral wings; teeth triangular, pointed. Posterior margin with tooth at each end near base of abdomen, sharper in males than in females, very low in adults, most slender and sharp in juveniles; third tooth of posterolateral wings extremely sharp and slender, pointed in juveniles.

FIGURE 135.—*Calappa sulcata* Rathbun. A, large chela in external view; B, female in dorsal view; 30 mm. indicated.

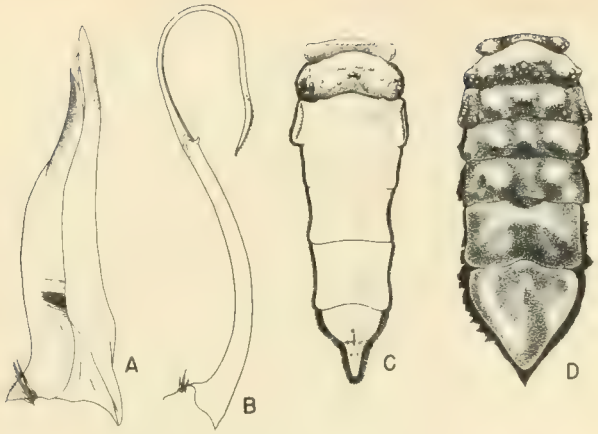

FIGURE 136.—*Calappa sulcata* Rathbun. A, male first pleopod in ventral view, approximately × 3; B, male second pleopod in dorsal (anterior) view, approximately × 3; C, abdomen of male, approximately × 0.8; D, abdomen of female, approximately × 0.6; A–C from near Margarita Island, Venezuela; D from Surinam (after Holthuis, 1958).

Chelipeds with outer surface of palm divided into three zones as in preceding species; large tubercles of lower zone low and inconspicuous; zones one, two, and three each separated by a row of sharply pointed tubercles; middle zone not extending horizontally, but curving dorsally in distal part, smooth, with minute granules; zone three smooth, except for two low, inconspicuous, granular tubercles near upper margin of palm; granulations on palm more distinct in females than in males; tooth on outer, lower, proximal surface of palm nearly rectangular in large individuals, slender and acute in smaller ones. Meral articles of walking legs with granules on lower surface.

Measurements.—Carapace: male, length, 77 mm., width, 98 mm.; female, length, 92 mm., width, 119 mm.

Color.—In alcohol, often light pinkish brown with small, narrow rings of dark red, median ring most conspicuous; each carpus with a ring, and each palm with one near upper margin enclosing tubercle toward proximal end of margin (Rathbun, 1937).

Habitat.—Twelve to 100 fathoms (Cerame-Vivas, personal communication).

Type locality.—Off Louisiana, lat. 29°24′30″ N., long. 88°01′ W., depth, 35 fathoms.

Known range.—Cape Hatteras, N.C., to Gulf of Mexico; through West Indies to French Guiana.

Remarks.—Hildebrand (1954) reported this species (under the name *C. springeri*) as conspicuous but never abundant in the western and northwestern Gulf of Mexico at depths of 12 to 35 fathoms. One ovigerous female was found in May off Padre Island, Tex.

Genus *Acanthocarpus* Stimpson, 1871

Rathbun, 1937, p. 220.

Acanthocarpus alexandri Stimpson

Figure 137

Acanthocarpus alexandri Stimpson, 1871a, p. 153.—Rathbun, 1937, p. 221, pl. 69, figs. 1–2 (rev.).

Recognition characters.—Carapace ovate, regularly convex, widest in anterior half; surface uneven, granulate, and punctate, with protuberances arranged longitudinally in roughly five rows centrally, and two shorter, intercalated rows behind orbits; all rows formed into ridges, those adjacent to midline each terminating in a spine on posterolateral margin. Posterior margin arcuate bearing a low eminence at middle; inferior margin of pterygostomian region with a row of 7 to 11 strong, widely spaced, oblique ridges of varying length. Orbits large, margins ciliated.

Chelipeds strong; merus bispinose on distal outer surface, inferior spine strong and a little longer or shorter than half width of carapace, superior spine one-fourth to one-third length of inferior spine; hand with superior crest of 7 closely placed teeth, and an oblique 6-toothed crest on outer surface extending from base of dactyl to posteroinferior angle, scattered tubercles between crests; inner surface of hand with stridulating ridge composed of about 45 oblique, closely placed striae which can be played against oblique ridges of peterygostomian region. Walking legs smooth. Sternal plastron with a conical tubercle on either side of first article.

Measurements.—Male carapace: length, 13 mm.; width, 32 mm.

Color.—Dorsal surface of carapace and chelipeds pale reddish orange, deepest in hue on elevations of carapace and bases of meral spines of chelipeds; underparts white, slightly tinged with red (Rathbun, 1937).

Habitat.—Thirty-seven to 208 fathoms.

FIGURE 137.—*Acanthocarpus alexandri* Stimpson. Male in dorsal view, walking legs of left side not shown, 10 mm. indicated.

Type locality.—Off the Quicksands, Florida Keys, 74 fathoms.

Known range.—Georges Bank off Massachusetts to west coast of Florida; Puerto Rico to Grenadines; Brazil (Da Costa, 1959).

Remarks.—The species has been recorded off both Carolinas, usually at depths greater than 100 fathoms. One collection was taken off South Carolina in 1950 at 60–65 fathoms along with *Sicyonia* and *Hymenopenaeus* sp.

Rathbun (1937) reported ovigerous females in June and July from Florida.

Subfamily **Matutinae**

Merus of external maxillipeds elongate and acute, entirely concealing palp in repose (Alcock *in* Rathbun, 1937).

Genus ***Hepatus*** Latreille, 1802

Rathbun, 1937, p. 234.—Holthuis, 1959, p. 173.

KEY TO SPECIES IN THE CAROLINAS

a. Carapace covered with small spots; front bidentate *pudibundus* (p. 157).

aa. Carapace covered with large spots; front truncate *epheliticus* (p. 158).

Hepatus pudibundus (Herbst)

Figures 138–139

Cancer pudibundus Herbst, 1785, p. 199.

Hepatus princeps: Rathbun, 1937, p. 235, pl. 70, figs. 1–2 (rev.).

Hepatus pudibundus: Holthuis, 1959, p. 167, figs. 36–38a, b (rev.).

Recognition characters.—Carapace between two-thirds and three-fourths as long as broad, relatively narrower in juveniles than in adults, covered with transverse lines or small spots, strongly convex. Surface smooth in adults; juveniles with eight distinct rows of tubercles, three in a transverse line in broadest part of carapace, two others in front and three behind. Front thick, obtuse, slightly bidentate. Anterolateral margin divided into 12 or 13 more or less rectangular teeth, denticulate on margins and not projecting; anterior portion of posterolateral margin consisting of 2 rows of tubercles placed side by side with no space between, a small tooth in middle of rows and another in posterior portion of this margin.

Outer face of hands with five rows of tubercles exclusive of marginal ones. Dactyls of walking legs with a coating of short, dense pubescence, except for tip, and a narrow smooth line on each side.

Measurements.—Carapace: males, length, 16–55 mm., width, 21–76 mm.; females, length, 14–46 mm., width, 18–62 mm. (Holthuis, 1959).

Color.—"Pale yellowish brown, with dark-brown transverse lines, or transverse series of spots; legs subochreous [sic], with one or two large purplish blotches in each joint." (Dana *in* Rathbun, 1937.) Holthuis (1959) gave the color in preserved specimens. Carapace covered with small reddish dots, scattered or sometimes arranged into transverse bands or lines, larger posteriorly than anteriorly; similar dots on carpus and palm; walking legs with two conspicuous broad bands of reddish color on merus, one on carpus and one on propodus, meral bands most distinct on last leg.

FIGURE 138.—*Hepatus pudibundus* (Herbst). Female in dorsal view, approximately natural size (after Holthuis, 1959).

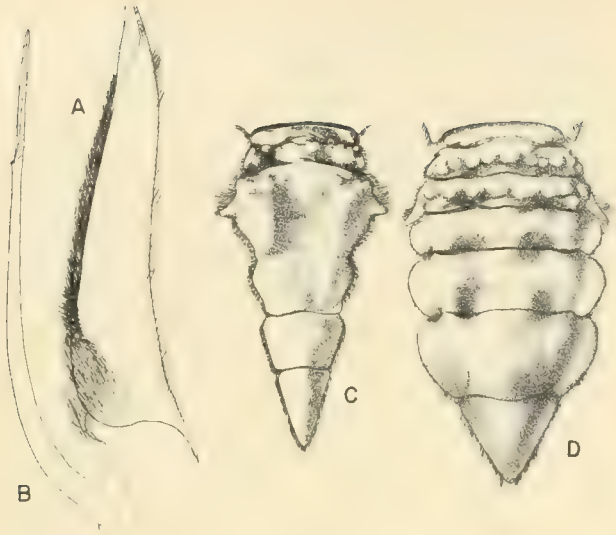

FIGURE 139.—*Hepatus pudibundus* (Herbst). A, male first pleopod; B, male second pleopod; A–B approximately × 8; C, abdomen of male; D, abdomen of female; C–D approximately × 2 (after Holthuis, 1959).

Habitat.—Beach to 6 fathoms.

Type locality.—Martinique.

Known range.—Georgia to State of São Paulo, Brazil.

Remarks.—Holthuis (1959) reported an ovigerous female in April from Surinam. Several of the specimens Holthuis studied carried one or more sea anemones on the carapace and one bore barnacles.

Hepatus epheliticus (Linnaeus) Calico crab, Dolly Varden crab

Figure 140

Cancer epheliticus Linnaeus. 1763, p .414.
Hepatus epheliticus: Hay and Shore, 1918, p. 422, pl. 37, fig. 1.—Rathbun, 1937, p. 238, pl. 70, figs. 3–4; pl. 71, figs. 1–4 (rev.).

Recognition characters.—Carapace covered with large spots, about two-thirds as long as wide, convex above, regularly arcuate in front, strongly narrowed behind, almost smooth, with indistinct lines of low granules on gastric region and posterior part of branchial region. Front narrow, truncate, tuberculate, not dentate, and placed higher than continuation of anterolateral borders of carapace; anterolateral borders dentate with denticles more prominent than in *H. pudibundus*, middle denticle of each tooth projecting.

Chelipeds moderately strong; carpus and hand with lines of coarse tubercles on outer face and a three- to four-toothed crest on superior margin of hand. Dactyls of walking legs with a coating of short, dense pubescence except for tip and a narrow smooth line on each side.

Measurements.—Carapace of male: length, 46 mm.; width, 67 mm.

Variations.—In a series representing various ages a great deal of variation is shown, the granulations being relatively much coarser and the spots more numerous and variable in color in juveniles.

Color.—Dark gray or brownish with numerous, rather large, round or irregular spots of light red (muddy lavender to light red in young) with darker borders scattered over carapace.

Habitat.—This species is often found in depths of a few fathoms in channels of Beaufort, N.C., harbor, though such individuals are not so numerous or large as those taken in the ocean outside. Gunter (1950) found the species in water ranging from 28.7 to 35.2‰. Two to 25 fathoms.

Type locality.—Carolina.

Known range.—Chesapeake Bay to Gulf of Campeche, Mexico; Cuba; Jamaica; Dominican Republic.

Remarks.—Though recorded in depths to 25 fathoms, Hildebrand (1954, 1955) found this species most common shoreward of 12 fathoms in

FIGURE 140.—*Hepatus epheliticus* (Linnaeus). Male in dorsal view, legs of left side not shown, 20 mm. indicated.

Texas and Mexico. He found ovigerous females rare, but occurring in July, and noted a common occurrence of the sea anemone, *Calliactis tricolor*, on the carapace, as found also by Carlgren and Hedgpeth (1952).

Gray (1957) found that *H. epheliticus* has a large gill area in relation to its weight. He related this large respiratory area to its active nature as compared to other strictly aquatic crabs.

Costlow and Bookhout (1962b) described five zoeal and one megalops stage from individuals hatched and reared at 25° C. in an array of salinities ranging from 20 to 40 °/₀₀. Complete development took place only at 30 and 35 °/₀₀ though some growth occurred in the other salinities. The authors pointed out that the adults are usually found in waters with salinity in the 30–35 ‰ range.

Genus *Osachila* Stimpson 1871

Rathbun, 1937, p. 248.—Hemming, 1958b, p. 17.

KEY TO SPECIES IN THE CAROLINAS

a. Posterolateral margin of carapace thin edged, almost sharp ..... *tuberosa* (p. 159).

aa. Posterolateral margin of carapace thick, blunt ..... *semilevis* (p. 159).

Osachila tuberosa Stimpson

Figure 141

Osachila tuberosa Stimpson, 1871a, p. 154.—Hay and Shore, 1918, p. 423, pl. 31, fig. 10.—Rathbun, 1937, p. 250, pl. 77, fig. 3 (rev.).

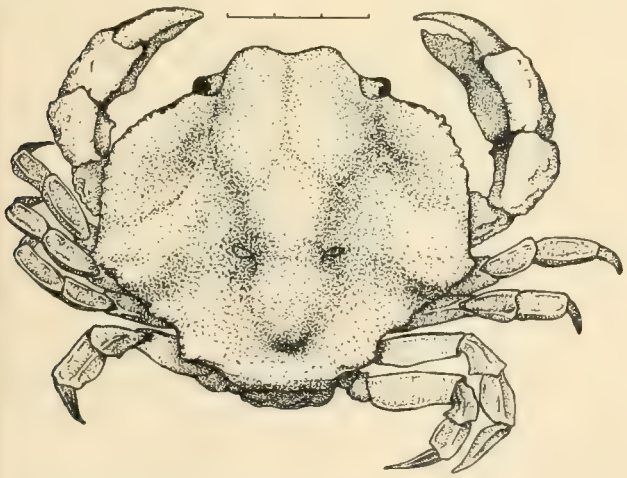

FIGURE 141.—*Osachila tuberosa* Stimpson. Male in dorsal view, 3 mm. indicated.

Recognition characters.—Carapace octagonal, with six large protuberances, one mesogastric, paired metagastric, one cardiac, paired mesobranchial; protuberances and lateral margins finely eroded. Anterolateral margins finely dentate, continued toward buccal cavity; posterolateral margins thin edged, with four lobes, first lobe projecting sideways slightly beyond adjacent anterolateral tooth. Front usually with a narrow sinus. Maxillipeds, sternum, abdomen, and bases of legs eroded.

Chelipeds short, thick, tuberculate on outer face, and with rough margins; hand stout, upper margin with three teeth, proximal one bifid; immovable finger thick. Walking legs more or less prismatic with sharp margins and light longitudinal grooves.

Measurements.—Carapace of female: length, 18 mm.; width, 20 mm.

Color.—"Sand color with reddish cast, white below, claws and legs white." (Henderson *in* Rathbun, 1937.)

Habitat.—Forty to 65 fathoms.

Type locality.—Five stations among the Florida reefs, 36–68 fathoms.

Known range.—Off Cape Hatteras, N.C., to west Florida.

Remarks.—This southern species has been recorded only once from North Carolina.

Osachila semilevis Rathbun

Figure 142

Osachila semilevis Rathbun, 1916, p. 652, pl. 36, fig. 1.—Hay and Shore, 1918, p. 422, pl. 31, fig. 9.—Rathbun, 1937, p. 251, pl. 77, fig. 1 (rev.).

Recognition characters.—Much like *O. tuberosa.* Carapace octagonal, with six large protuberances, one mesogastric, paired metagastric, one cardiac, paired mesobranchial; protuberances eroded, depressions nearly smooth. Anterolateral margins finely dentate, continued toward buccal cavity; posterolateral margins thick, with four lobes; first lobe not projecting laterally so far as adjacent anterolateral lobe; last lobe quite prominent. Front usually with a narrow buttonholelike sinus.

Chelipeds short, thick, tuberculate on outer face and with rough margins; hand stout, upper margin with three simple teeth; immovable finger thick, dactyl comparatively slender and straight. Walking legs of moderate size, more or less

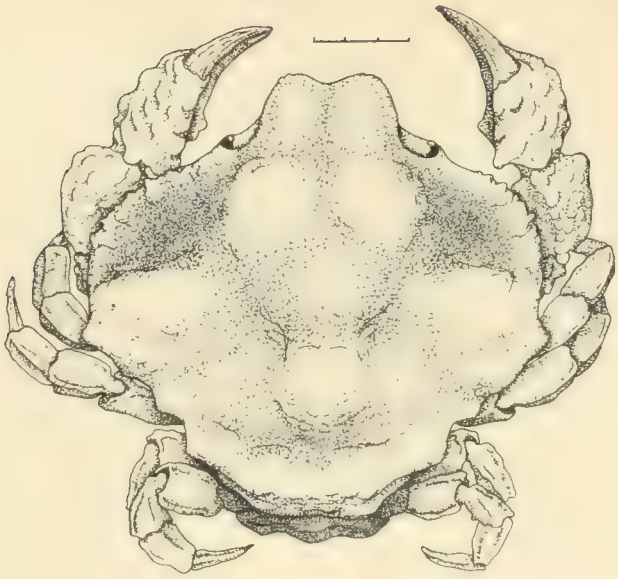

FIGURE 142.—*Osachila semilevis* Rathbun. Animal in dorsal view, 3 mm. indicated.

prismatic and lightly grooved. Abdomen narrow, eroded along margins and on last two segments.

Measurements.—Carapace of ovigerous female: length, 13 mm.; width, 15 mm.

Habitat.—Thirteen to 50 fathoms.

Type locality.—Gulf of Mexico, 25 fathoms.

Known range.—Off Beaufort, N.C., to northwest Florida.

Remarks.—This southern species has been recorded north of Florida only twice, both times from the Beaufort, N.C., area. Ovigerous females have been taken from Florida in July.

Subsection **Brachygnatha**

Brachyura having buccal frame roughly quadrate. Last pair of legs normal in form, rarely reduced in size, and almost never dorsal. Gills few. First abdominal appendages of female absent, female openings sternal.

Superfamily **Brachyrhyncha**

Fore part of body broad, rostrum reduced or absent; body oval, round, or square, usually broader than long. Orbits nearly always well enclosed.

Family ***Portunidae***. The swimming crabs

Crabs with body transversely oval, usually five to nine lateral teeth. Last pair of legs usually distinctly adapted for swimming, with terminal article ovate, flattened.

The family has a fossil record in America dating from the Cretaceous (Rathbun, 1935).

Stephenson and Campbell (1960) discussed the status of portunid subfamily names in the light of recent action by the International Commission on Zoological Nomenclature. This decision altered the usage of Rathbun (1930a) in that the subfamilies Liocarcininae and Thalamitinae become respectively Macropipinae and Portuninae.

KEY TO GENERA AND SOME SPECIES IN THE CAROLINAS

a. Carapace with five teeth of about equal size on anterolateral margin; interocular teeth three (Subfamily Macropipinae) ..... *Ovalipes* (p. 160).

aa. Carapace with nine anterolateral teeth, lateral tooth usually much larger than others; interocular teeth four, six, or eight (Subfamily Portuninae).

b. Movable portion of antenna not excluded from orbit.

c. Palate with longitudinal ridge.

d. Abdomen of male more or less triangular ..... *Portunus* (p. 162).

dd. Abdomen of male with last two segments much narrower than basal segments ..... *Callinectes* (p. 168).

cc. Palate without logintudinal ridge ..... *Arenaeus cribrarius* (p. 173).

bb. Movable portion of antenna excluded from orbit by prolongation of basal article; anterolateral teeth alternately large and small ..... *Cronius ruber* (p. 174).

Subfamily **Macropipinae**

Genus ***Ovalipes*** Rathbun, 1898

Rathbun, 1930a, p. 18.

KEY TO SPECIES IN THE CAROLINAS

a. Carapace yellowish gray, closely set with small annular spots of reddish purple; iridescent spots between each pair of anterolateral spines approximately alike in size and shape ..... *ocellatus* (p. 160.)

aa. Carapace yellowish gray, without ocellated spots; iridescent spot between fourth and fifth anterolateral spines large and nearly semicircular in shape ..... *guadulpensis* (p. 161).

Ovalipes ocellatus (Herbst)

Figure 143

Cancer ocellatus Herbst, 1799, p. 61, pl. 49, fig. 1.
Ovalipes ocellatus ocellatus: Hay and Shore, 1918, p. 426, pl. 32, fig. 7.—Rathbun, 1930a, p. 19, pls. 2–3 (rev.).
Ovalipes ocellatus: Williams, 1962, pp. 39–41.

Recognition characters.—Carapace about one-fourth wider than long, convex, finely granulate

FIGURE 143.—*Ovalipes ocellatus* (Herbst). Male in dorsal view, approximately × 0.80 (after Rathbun, 1884).

overall except for longitudinal band of slightly enlarged granules in median line and smooth area on posterior central portion of adults. Front with three acute teeth, median one about twice as long as lateral ones. Orbit with a shallow fissure above, often nearly closed in adults, open in young. Five anterolateral teeth strong, acute, directed forward; inner suborbital angle projecting at least as far as median frontal tooth. Pterygostomian region with a long, curved, stridulating ridge made up of approximately 50 close-set striae narrowing into tubercles at inner end of ridge, a short complementary ridge on proximal end of inner margin of merus; lobe at distal inner angle of merus of outer maxilliped longer than broad.

Chelipeds rather large; distal three-fifths of anterior margin of merus with several small spines and a dense fringe of hair; carpus with two spines, inner one very long; hand triangular in section, external border costate, covered with uniform small tubercles, internal border with an overhanging densely hairy ridge ending distally in a sharp spine, ridges and internal line of hairs continued on dactyl; fingers about as long as palm, tapering gradually, tips turned abruptly toward each other.

Abdomen of male narrow, sides nearly parallel; sixth segment nearly twice as long as seventh in midline, seventh segment subcircular; first pleopods of male broad and stout in proximal two-thirds, narrowing abruptly distally and with terminal portion bent ventrolaterally in a sinuous curve. Abdomen of adult female suboval and small compared to sternum.

Measurements.—Carapace: males, length, 64 mm., width, 77 mm.; female, length, 39 mm., width, 48 mm.

Variations.—Spines are more acute on young than on old individuals, and on some old adults the anterolateral spines are worn away leaving only rounded humps. The orbital fissure is nearly closed in adults but often open in young individuals. The width between the suborbital angles tends to increase relatively with age.

Color.—"Yellowish gray, closely set with small annular spots of reddish purple; carapace and chelipeds with a silvery or brassy iridescence; ground color of chelipeds and legs light brownish tending to orange and bluish; large irregular bluish purple spots on upper surface of chelipeds; large part of carpus including spine bluish; similar but lighter spots on proximal half of other legs; paddles greenish yellow, with deep yellow rim" (Rathbun, 1930a, and other authors). An iridescent spot between each pair of anterolateral spines.

Habitat.—Common on a variety of bottoms, especially sand; surface to 18 fathoms.

Type locality.—Long Island near New York.

Known range.—Prince Edward Island, Canada (E. L. Bousfield, personal communication), to Charleston, S.C., and on Texas coast jetties (Whitten, Rosene, and Hedgpeth, 1950).

Remarks.—The distinctions between this species and *O. guadulpensis* were discussed by Williams (1962). There is a distinct color difference, pointed out in the color descriptions, and an apparent difference in habitat among the adults. Adults of *O. ocellatus* are found near shore in the Carolinas where the young of both species are also found, as pointed out by a number of authors.

Pearse, Humm, and Wharton (1942) pointed out that *O. ocellatus* can bury itself completely in sand and respire by passing water into the gill cavity from anterior lateral openings, then out through two posterior openings. Gray (1957) correlated great activity of the species with large gill area and compared this with gill areas of other strictly aquatic crabs.

Ovalipes guadulpensis (Saussure)

Portunus guadulpensis Saussure, 1858, p. 433, pl. 2, fig. 10.
Ovalipes ocellatus floridanus Hay and Shore, 1918, p. 427, pl. 32, fig. 8.
Ovalipes ocellatus guadulpensis: Rathbun, 1930a, p. 23, pl. 4 (rev.).
Ovalipes guadulpensis: Williams, 1962, pp. 39–41.

Recognition characters.—Closely resembling *O. ocellatus*, but differing in the following characters: dorsal aspect of carapace not covered with ocellated spots; body flatter than *O. ocellatus*, and carapace evenly granulate overall except for smooth area on rear central portion; outer orbital and frontal teeth more acute than in *O. ocellatus*, median frontal tooth acuminate; iridescent spot between fourth and fifth anterolateral spines larger than spots between first to fourth teeth and nearly semicircular in shape; external ridge on palm of chelipeds with tubercles not uniform in size giving a roughened appearance in individuals larger than 30 mm. in width.

Measurements.—Carapace: male, length, 67 mm., width, 82 mm.; female, length, 56 mm., width, 67 mm.

Variations.—The distance between the suborbital angles tends to increase relatively with age.

Color.—"General color of carapace light lavender gray underlaid with dull yellow, some specimens darker or lighter, with a regular pattern of lighter spots dull yellow, off white, or bluish yellow to lavender yellow, rear border of carapace light blue; spines of carapace purplish red at base to red or purple subdistally, white at tips; carpus and merus of chelipeds somewhat same color as carapace except pink flesh colored at carpo-meral joint and on hand; fingers white on inner surface, and with white teeth; large spine at internal angle of carpus and a few small but distinct spots on superoexternal surface of hand purple, large spine grading to lighter purple on body of carpus; anterior border of chela and first three pairs of walking legs with a longitudinal band of brownish purple, band extending to lower border of dactyl on chela; dactyls of first three walking legs and outer border of hand immediately below external ridge, same color, sometimes darker on dactyl with teeth same color, distal tip of immovable finger similarly colored; blade of swimming leg yellowish; underparts light.

"Iridescent spots between anterolateral teeth, on distal or dorsal surface of external carpal spine and along upper edge of hand, at superodistal corner of merus on first three walking legs and along dorsal edge of first three pairs of walking legs distally, or dorsal surface of second abdominal segment; spot between fourth and fifth anterolateral spines nearly semicircular" (Williams, 1962).

Habitat.—Taken on sandy bottom in the Carolinas and from similar bottoms elsewhere, according to literature records; surface to 49 fathoms (rarely to 925 fathoms?).

Type locality.—Guadeloupe.

Known range.—Cape Hatteras, N.C., to Port Aransas, Tex.; Guadeloupe; Brazil.

Remarks.—The distinctions between this species and *O. ocellatus* were discussed by Williams (1962). There is a distinct color difference, pointed out in the color descriptions, and an apparent difference in habitat among the adults. Adults of *O. guadulpensis* are found farther from shore than adults of *O. ocellatus* in the Carolinas, but the young of both species are found near shore, as pointed out by a number of authors.

Ovigerous females are known from North Carolina in January.

Subfamily **Portuninae**

Genus ***Portunus*** Weber, 1795

Rathbun, 1930a, p. 33.—Hemming, 1958b, p. 133.—Stephenson and Campbell, 1959, p. 85.

Stephenson and Campbell (1959) gave a number of arguments for and against the utility of subgeneric limitations within this genus as now understood. Though subgeneric subdivisions may be useful in the limited Carolinian fauna, they are being deleted here.

KEY TO SPECIES IN THE CAROLINAS

a. Carapace wide; anterolateral margins forming arc of a circle with center near posterior margin of carapace.
  b. Interocular teeth six, inner orbital tooth being entire.
    c. Carapace convex, mostly smooth and glossy; palms swollen, only one spine on upper margin in addition to spine at base of dactyl_____*sayi* (p. 163).
    cc. Carapace uneven, not smooth and glossy; two spines on upper margin of palm in addition to spine at base of dactyl_____*anceps* (p. 163).
  bb. Interocular teeth eight, inner orbital tooth being bilobed_____*gibbesii* (p. 164).
aa. Carapace narrow; anterolateral margins forming arc of a circle with center near middle of cardiac region.
  b. Interocular teeth eight, inner orbital tooth being bilobed_____*spinimanus* (p. 165).
  bb. Interocular teeth six, inner orbital tooth being entire or notched laterally.
    c. Superoexternal surface of chela with a conspicuous, smooth, silvery, or iridescent area
ordwayi (p. 166).

cc. Superoexternal surface of chela ridged and not iridescent.

d. Last pair of legs with posterodistal margin of merus unarmed; upper margin of dactyl conspicuously fringed with long hairs
depressifrons (p. 163).

dd. Last pair of legs with posterodistal margin of merus armed with spinulous lobe; carpus of cheliped with inner spine greatly elongated
spinicarpus (p. 167).

Portunus sayi (Gibbes)

Figure 144

Lupa sayi Gibbes, 1850, p. 178.
Portunus sayi: Hay and Shore, 1918, p. 428, pl. 33, fig. 2.—Rathbun, 1930a, p. 37, text-figs. 6–7; pl. 14 (rev.).

Recognition characters.—Carapace nearly twice as wide as long, somewhat tumid, smooth and polished to naked eye, finely granulate under magnification. Six frontal teeth including inner orbitals, two submedian teeth smaller but on a line with next pair. External orbital tooth larger than those of anterolateral border except stout, acute ninth; remaining anterolateral teeth blunt and increasing slightly in size posteriorly.

Chelipeds of moderate length, somewhat larger in males than in females; merus with four, rarely three, stout, curved spines in front, none behind; carpus with two spines; hand with an acute spine at articulation and a smaller one near base of movable finger; external surface with two longitudinal ribs with lowermost extending on finger; superior surface with three ribs continuing on finger, innermost one with fringe of hair beneath.

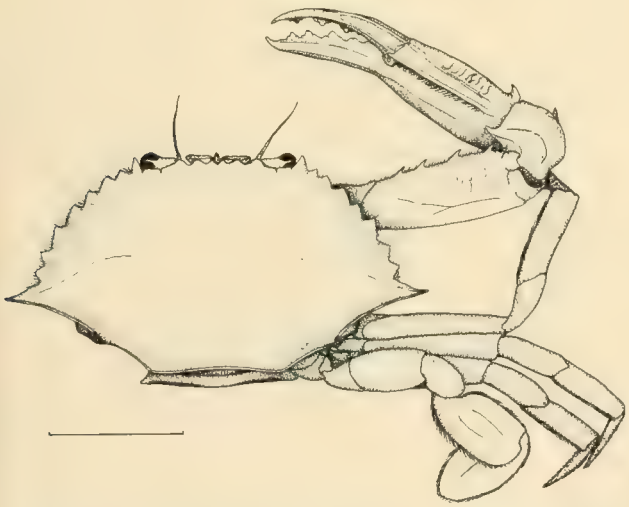

FIGURE 144.—*Portunus sayi* (Gibbes). Animal in dorsal view, legs of left side not shown, 20 mm. indicated.

Measurements.—Carapace: male, length, 27 mm.; width, 53 mm.

Color.—Chocolate brown or purplish with cloudings of olive green or light brown and irregular white or flesh-colored spots; orange margins on spines of chelipeds.

Habitat.—Normally this is a pelagic form living among floating *Sargassum*, but it is often carried into Beaufort Inlet, N.C., by currents.

Known range.—North Atlantic Ocean from Nova Scotia south through Gulf of Mexico to Brazil; mid-Atlantic Ocean; Bermuda; Kerguelen Island, south Indian Ocean.

Remarks.—The species has a fossil record dating from the lower Miocene of North America (Rathbun, 1935).

Ovigerous females are known from April to August in the southeastern United States and in parts of the West Indies. They are also known from Culebra in February and near Nantucket in September (Rathbun, 1930a, in part). Some of the larval stages were described by Lebour (1944) at Bermuda. Coventry (1944) gave new records for the Bahamas in addition to those listed by Rathbun (1930a).

Portunus anceps (Saussure)

Figure 145

Lupea anceps Saussure, 1858, p. 434, pl. 2, figs. 11–11b.
Portunus anceps: Hay and Shore, 1918, p. 431, pl. 33, fig. 8.—Rathbun, 1930a, p. 42, pl. 15 (rev.).

Recognition characters.—Carapace twice as wide as long, pubescent, and with several indistinct, arching, granulate, transverse ridges. Six frontal teeth including inner orbitals, inner orbitals blunt and considerably shorter than outer pair of true frontal teeth, submedian teeth short, smaller than inner orbitals. Anterolateral teeth small, acute, curved forward, last one sharp, slender, and about as long as space occupied by four preceding teeth.

Chelipeds long; merus with four spines in front, a distal one behind; carpus ridged, with a strong internal and a smaller external spine; hand with ridges on outer and superior surfaces, most of ridges continuing on fingers, superointernal ridge more elevated than others, ending distally in two spines, one behind other.

Measurements.—Carapace: male, length, 13 mm., width, 26 mm.; ovigerous female, length, 15 mm., width, 29 mm.

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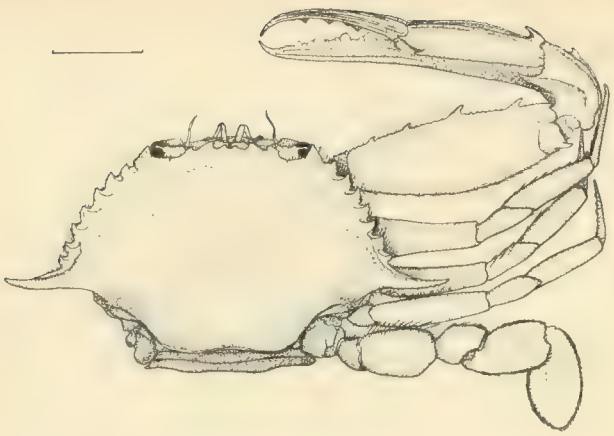

FIGURE 145.—*Portunus anceps* (Saussure). Male in dorsal view, legs of left side not shown, 5 mm. indicated.

Color.—Mottled gray and yellowish white so as to imitate sand; first pair of legs red or yellow; chelipeds and other legs same color in part (Verrill, 1908). Hairs on legs colorless (Abramowitz, 1935).

Habitat.—This form lives on or near sandy shores in tropical waters, but is sometimes carried northward in the Gulf Stream to the North Carolina capes; surface to 40 fathoms.

Type locality.—Cuba.

Known range.—Cape Hatteras, N.C., to Brazil; Bermuda.

Remarks.—Rathbun (1930a) recorded ovigerous females from June in Cuba to October in North Carolina.

Portunus gibbesii (Stimpson)

Figure 146

Lupa gibbesii Stimpson, 1859, p. 57.
Portunus gibbesii: Hay and Shore, 1918, p. 428, pl. 33, fig. 1.—Rathbun, 1930a, p. 49, pls. 16–17 (rev.).

Recognition characters.—Carapace approximately twice as wide as long, not tumid, thickly covered with small spherical granules, pubescent, and with three or four naked, transverse ridges, two of which arise from lateral spines and run toward gastric region. Eight frontal teeth including two points of each inner orbital, median pair of frontal teeth narrower and slightly more advanced than next pair. External orbital tooth not much larger than teeth of anterolateral border, these latter stout, acute, directed forward; last tooth, or lateral spine, slender, sharp, curved forward and about as long as space occupied by three preceding teeth. One or more small, naked, iridescent areas near anterolateral margin at base of teeth.

Chelipeds long, slender; merus with five to seven spines in front, and one behind at distal end; carpus with a large internal and a smaller external spine; hand slender, ribbed on all surfaces; ribs continued on fingers and roughened by sharp-pointed, appressed tubercles; hand with two spines, one at articulation with carpus, another near distal end of superior rib; fingers nearly straight with incurved tips.

Measurements.—Carapace: male, length, 29 mm.; width, 61 mm.

Color.—Brownish red, transverse ridges on carapace, spines, and margins of chelipeds carmine red; front side of legs brilliantly iridescent by lantern light, iridescence evident to some extent in preserved material.

Habitat.—The species is fairly common about the Beaufort, N.C., region and is often taken in deeper channels of the harbor. Along with *P. spinimanus*, Hildebrand (1955) reported this species as common on the shrimping grounds on Campeche Bank in the Gulf of Mexico, but rare on the Texas coast. Surface to 48 fathoms, rarely deeper.

Type locality.—South Carolina and St. Augustine, Fla.

Known range.—Southern Massachusetts to Texas; Venezuela; Surinam.

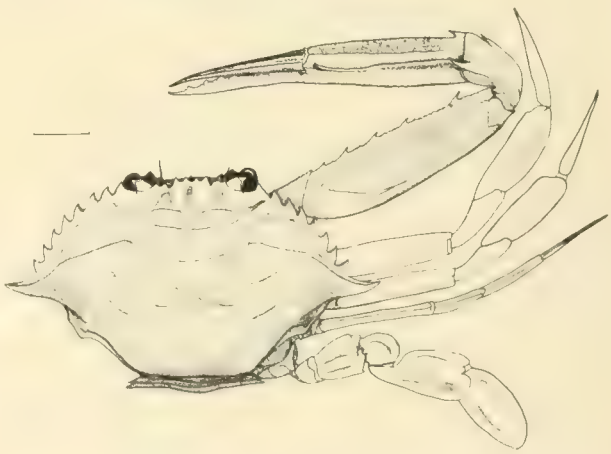

FIGURE 146.—*Portunus gibbesii* (Stimpson). Male in dorsal view, legs of left side not shown, 10 mm. indicated.

Remarks.—Ovigerous females have been reported and are otherwise known to occur in the months February to June from North Carolina to Surinam (Holthuis, 1959; Rathbun, 1930a).

Gray (1957) computed gill area per unit weight for *P. gibbesii* as intermediate among a number of swimming crabs studied.

Portunus spinimanus Latreille

Figure 147

Portunus spinimanus Latreille, 1819, p. 47.—Hay and Shore, 1918, p. 429, pl. 33, fig. 4.—Rathbun, 1930a, p. 62, text-fig. 10, pls. 26–28 (rev.).

Recognition characters.—Carapace considerably less than twice as wide as long, finely granulate and pubescent, with a number of prominent, curved, coarsely granulate, transverse ridges. Eight frontal teeth, including inner orbitals, each notched at summit and presenting two points; median pair of teeth slightly narrower and more advanced than next pair, all considerably more advanced than inner orbitals. Outer orbital teeth obtuse, not much larger than teeth of anterolateral borders, these latter strong, acute, or acuminate, about equal in size except last; this tooth about twice as large as others and usually curved forward.

Chelipeds long, pubescent, serratogranulate all over; merus with four, occasionally five, strong, curved spines in front and one at distal end; carpus with two spines, inner one much stronger, and with four conspicuous ridges on upper surface; hand slender, all surfaces with ridges which extend on fingers; a strong spine at carpal articulation and another near base of dactyl; fingers nearly straight, tips incurved.

Measurements.—Carapace: female, length, 55 mm.; width, 88 mm.

Variations.—Large males have relatively longer, thinner chelipeds and longer walking legs than large females.

Color.—Pubescence yellowish or reddish brown, ridges of carapace, spines of chelipeds, fingers and tips of legs reddish brown; anterolateral teeth reddish at base, white at tips; merus, carpus, and hand of chelipeds with white blotches.

Habitat.—This species is common in the waters off Beaufort Inlet, N.C., and is sometimes found in deeper channels of the harbor. *P. gibbesii* is often found in company with *P. spinimanus*. A similar association of these two species was reported by Hildebrand (1955) for the Campeche Banks in the Gulf of Mexico where they are common. On beach under *Sargassum;* surface to 50 fathoms.

FIGURE 147.—*Portunus spinimanus* Latreille. Male in dorsal view, legs of left side not shown, 20 mm. indicated.

Type locality.—American waters, common in Brazil.

Known range.—New Jersey through Gulf of Mexico and West Indies to southern Brazil; Bermuda.

Remarks.—This species, which somewhat resembles *P. gibbesii*, can be readily distinguished from the latter by its narrower, rounder form, and by the entire lack of iridescent patches on the carapace mentioned for *P. gibbesii.*

Ovigerous females are known from January to July in Florida (Wass, 1955, in part); March in Campeche; April in Isle of Pines; May, August, and September in Surinam (Holthuis, 1959); and July in St. Thomas, V.I. (Rathbun, 1930a). Lebour (1950) found an ovigerous female among *Sargassum* in Bermuda in May, and from the eggs reared larvae which she illustrated.

Gray (1957) computed gill area per unit weight for *P. spinimanus* as intermediate among a number of swimming crabs studied.

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Portunus ordwayi (Stimpson)

Figure 148

Achelous ordwayi Stimpson, 1860a, p. 224.
Portunus ordwayi: Hay and Shore, 1918, p. 431, pl. 33, fig. 6. Rathbun, 1930a, p. 71, pl. 33 (rev.).

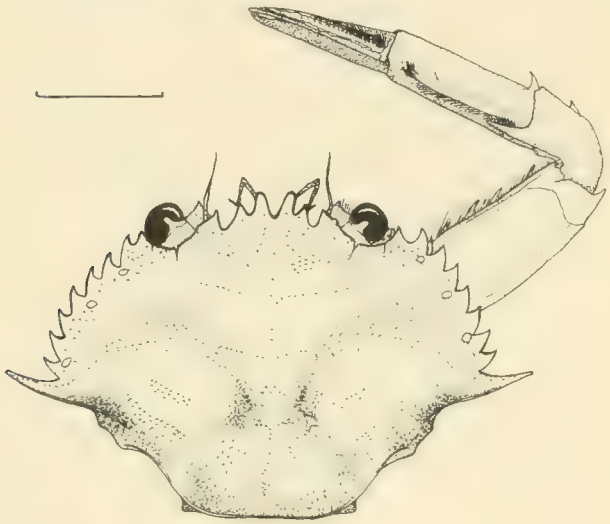

FIGURE 148.—*Portunus ordwayi* (Stimpson). Male in dorsal view, legs not shown except for right cheliped, 10 mm. indicated.

Recognition characters.—Carapace approximately 1.5 times as wide as long, uneven, elevations granulate and depressions pubescent, with a number of conspicuous, curving, transverse ridges. Six frontal teeth including acuminate inner orbitals; true frontal teeth about equal in size, triangular, acute, middle pair advanced beyond others. Outer orbital tooth large; anterolateral teeth diminishing slightly in size from first to seventh, inclusive, eighth about as long as space occupied by two preceding teeth, tips of all acute and turned forward.

Chelipeds of moderate length; merus with four or five strong spines in front, a single distal one behind; carpus ribbed and with strong internal and much smaller external spine; hand ribbed on all surfaces except flat, highly iridescent, superior surface; superointernal ridge raised into a crest terminating distally in a sharp spine. Margins of carapace and chelipeds more or less fringed with silky hairs.

Measurements.—Carapace: male, length, 26 mm.; width, 42 mm.

Color.—Carapace and legs reddish brown due to fine mottling with red, yellowish brown, and gray; pale orange beneath, deeper orange on chelipeds and legs; chelae deep red brown above, fingers with two cross bands of light orange red. Blue coloration also apparent near red and dark pigments; hairs on appendages deep red (Abramowitz, 1935).

Habitat.—This is another of the tropical swimming crabs which move northward with warm water currents; surface to 58 fathoms, rarely deeper.

Type localities.—Key Biscayne and Tortugas, Fla.; St. Thomas, [V.I.].

Known range.—Vineyard Sound, Mass.; North Carolina through Gulf of Mexico, Caribbean Sea, and West Indies to State of Bahia, Brazil; Bermuda.

Remarks.—Rathbun (1930a) listed an ovigerous female in March from Florida.

Portunus depressifrons (Stimpson)

Figure 149

Amphitrite depressifrons Stimpson, 1859, p. 58.
Portunus depressifrons: Hay and Shore, 1918, p. 430, pl. 33, fig. 7.—Rathbun, 1930a, p. 84, pl. 41 (rev.).

Recognition characters.—Carapace approximately 1.6 times as wide as long, uneven, pubescent, and with indistinct transverse ridges. Six frontal teeth, including inner orbitals much larger than others, tips of all teeth about on a line. External orbital tooth strong, tip rounded; anterolateral teeth acute, turned forward, lateral tooth scarcely longer than one in front, teeth and intervals between them fringed with hairs.

Chelipeds trigonal, serratogranulate and pubescent; merus with five spines in front and a distal one behind; carpus with two spines, outer much smaller than inner one; hand short and compressed, upper margin raised into a crest terminating distally in a stout spine, a smaller spine at carpal articulation; fingers flattened, dactyl with border of hairs on superior margin. Walking legs unusually long and slender, first pair with articles fringed with hairs. Swimming legs shorter than in most species of genus.

Measurements.—Carapace: male, length, 26 mm.; width, 41 mm.

Color.—Carapace in life irregularly mottled with light and dark gray, closely imitating colors of sand; chelipeds and posterior legs similar, though paler; first pair of walking legs bright

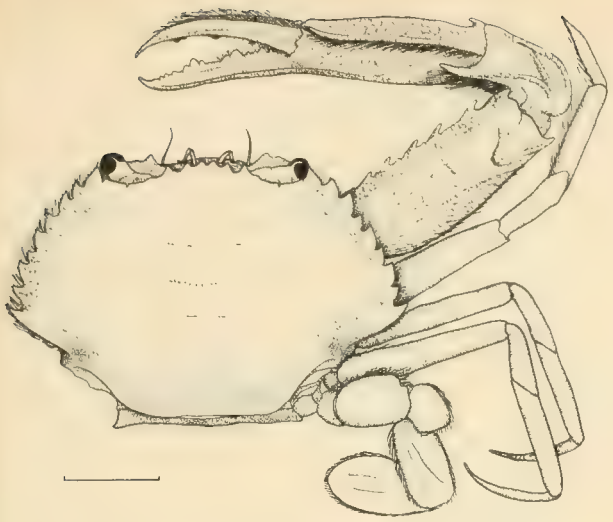

FIGURE 149.—*Portunus depressifrons* Stimpson. Male in dorsal view, legs of left side not shown, 10 mm. indicated.

purple, or deep blue in larger specimens, while some portion of same color usually apparent on next two pairs, but color of first pair in striking contrast with rest of crab. Very young specimens do not show this distinction in color of legs, so far as observed (Verrill, 1908).

Habitat.—Abundant in shallow water on sandy bottoms of coves and inlets at Bermuda (Verrill, 1908); surface to 16 fathoms.

Type localities.—South Carolina and Florida Keys.

Known range.—Fort Macon, N.C. (Coues and Yarrow, 1878; Kingsley, 1880) to Gulf of Campeche and Caribbean Sea; Bermuda.

Remarks.—This crab has not been collected in the Carolinas for many years, so far as recorded. Records in the U.S. National Museum show no specimens from farther north than Key West, Fla., and the Bahamas near the southeast coast of the United States. A number of specimens in the U.S. National Museum collection were taken from the stomachs of the gray snapper, *Lutjanus* (=*Neomaenus*) *griseus*, the yellow goatfish, *Mulloidichthyes* (=*Upeneus*) *martinicus*, and other predaceous fish. Rathbun (1930a) reported ovigerous females in June from Florida, and in August from Florida and the Caribbean. More recently, egg-bearing females have been taken on Campeche Banks in late August.

Portunus spinicarpus (Stimpson)

Figure 150

Achelous spinicarpus Stimpson, 1871a, p. 148.
Portunus spinicarpus: Hay and Shore, 1918, p. 429, pl. 33, fig. 3.—Rathbun, 1930a, p. 92, pl. 45.

Recognition characters.—Carapace slightly more than twice as wide as long, sculptured, with a number of naked, rather coarsely granulate, arching, transverse ridges separated by finely granulate and pubescent surfaces. Six frontal teeth, including inner orbitals, with sinuate but unnotched outer margins; true frontal teeth narrow, acute, separated by broad notches, median pair considerably advanced beyond others. External orbital tooth acute, larger than neighboring teeth of anterolateral margin; latter varying somewhat in size, concave sided, acute; lateral tooth with form of slender curving spine more than half as long as anterolateral border; posterolateral angle sharp, margin slightly recurved.

Chelipeds long, slender; merus with four or five stout, curved spines in front, and a single, similar, distal spine behind. Carpus with two spines, outer one small and weak, inner one long, extending along side of hand to near base of dactyl. Hand with serratotuberculate ridges, prolonged on fingers, and two spines, one at carpal articulation, another near base of movable finger. Fingers nearly straight, incurved at tips.

Measurements.—Carapace: male, length, 18 mm.; width, 38 mm.

Variations.—Rathbun (1930a) stated that ovigerous females are smaller than males, and their chelipeds are shorter, with the carpal spine not reaching beyond the superior spine of the hand. The lateral spine is relatively longer in young than in old individuals and changes in angle of projection with age, extending straight laterally or slightly backward in the young, but curving slightly forward in mature individuals.

Color.—Carapace buff pink, mottled, highest ridges touched with cinnamon red; fingers bordered with crimson and maroon; two basal teeth of dactyl and margin of palm white; rest of chela maroon purple and purplish red, same color on fringe of hair on carpal spine; walking legs purple. (Schmitt *in* Rathbun, 1930a, where great detail on younger individuals is given.)

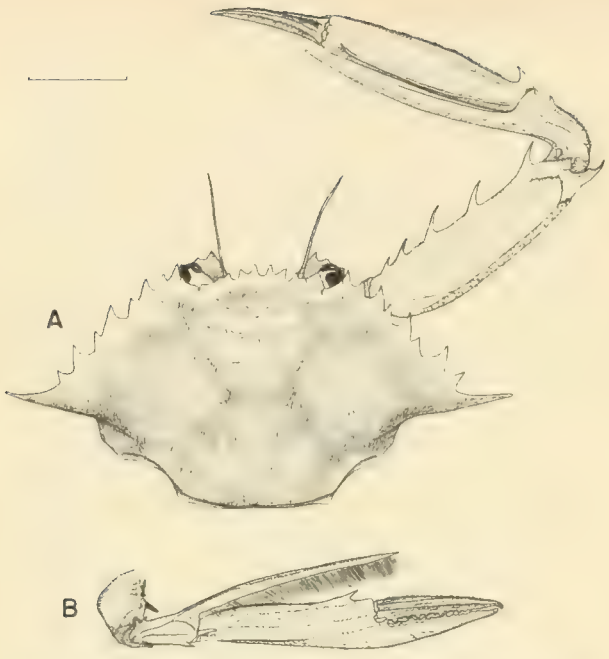

FIGURE 150.—*Portunus spinicarpus* (Stimpson). A, male in dorsal view, legs not shown except for right cheliped; B, right chela of male in frontal view; 5 mm. indicated.

Habitat.—This appears to be a species living in deeper waters of the region. On shrimping grounds in the western Gulf of Mexico, Hildebrand (1954) reported it as found only along the seaward side in depths of 15 to 37 fathoms. Five to 300 fathoms.

Type localities.—Off Tortugas, Carysfort Reef, Conch Reef, Alligator Reef, Pacific Reef, and American Shoal, Fla.; lat. 31°31′ N. long. 79° 41′ W. off Georgia; in depths ranging from 13 to 150 fathoms.

Known range.—Off Cape Hatteras, N.C., to State of São Paulo, Brazil.

Remarks.—Ovigerous females have been taken from January to September from Florida to Surinam, and in November in Texas. Pearse (1932b) found the barnacle, *Dichelastis sinvata* Aurivillius, on a number of individuals.

Genus ***Callinectes*** Stimpson, 1860

Rathbun, 1930a, p. 98.

KEY TO SPECIES IN THE CAROLINAS

a. Frontal teeth, including inner orbitals, four
sapidus (p. 168).

aa. Frontal teeth, including inner orbitals, six
ornatus (p. 172).

Callinectes sapidus Rathbun. Blue Crab

Figure 151

Lupa hastata Say, 1817, p. 65.

Callinectes sapidus Rathbun, 1896a, p. 352, pls. 12; 24, fig. 1; 25, fig. 1; 26, fig. 1; 27, fig. 1 (rev.).—Hay and Shore, 1918, p. 432, pl. 35, fig. 1.—Rathbun, 1930a, p. 99, pl. 47 (rev.).

Recognition characters.—Carapace, including lateral spines, 2.5 times as wide as long, moderately convex, nearly smooth, except lightly tuberculate on inner branchial and cardiac regions; a tuberculate transverse line from side to side between lateral spines, and a shorter transverse line about halfway between this and frontal margin. Four frontal teeth, including inner orbitals, triangular, acute, both pairs more or less distinctly bilobed. Anterior eight anterolateral spines of subequal length, concave on both margins and acuminate; lateral spines nearly straight, usually longer than space occupied by three preceding teeth; inner suborbital tooth prominent and acute.

Chelipeds of male large and powerful, smaller in female; merus with three spines in front and one small spine at distal end behind; carpus with one spine and one spiniform tubercle on external surface; hand strong, prominently ribbed, and with a strong proximal spine; fingers nearly straight and strongly toothed. Abdomen of male in form of inverted T; basal segments broad, distal segments narrow; penultimate segment constricted in proximal half, wider at both ends, terminal segment approximately oblong-lanceolate; first pleopods reaching nearly to, or beyond, extremity of abdomen, approximated through basal half, distal portions widely divergent except at tips. Immature female with abdomen triangular; mature female with abdomen broad, rounded, and lying loosely on ventral side of thoracic sterna.

Measurements.—Width of carapace (including spines): males, 200 mm.; females, 198 mm.; smallest mature females (excluding dwarfs), 86 mm. Exceptional males in water of low salinity may measure 230 mm., or more, in width.

Color.—Grayish, or bluish green of varying shades and tints, relieved by more or less red on spines of carapace; males with blue fingers on hands, mature females with red fingers on hands; underparts off white with tints of yellow and pink. Churchill (1919) gave a colored frontispiece showing ventral and other views.

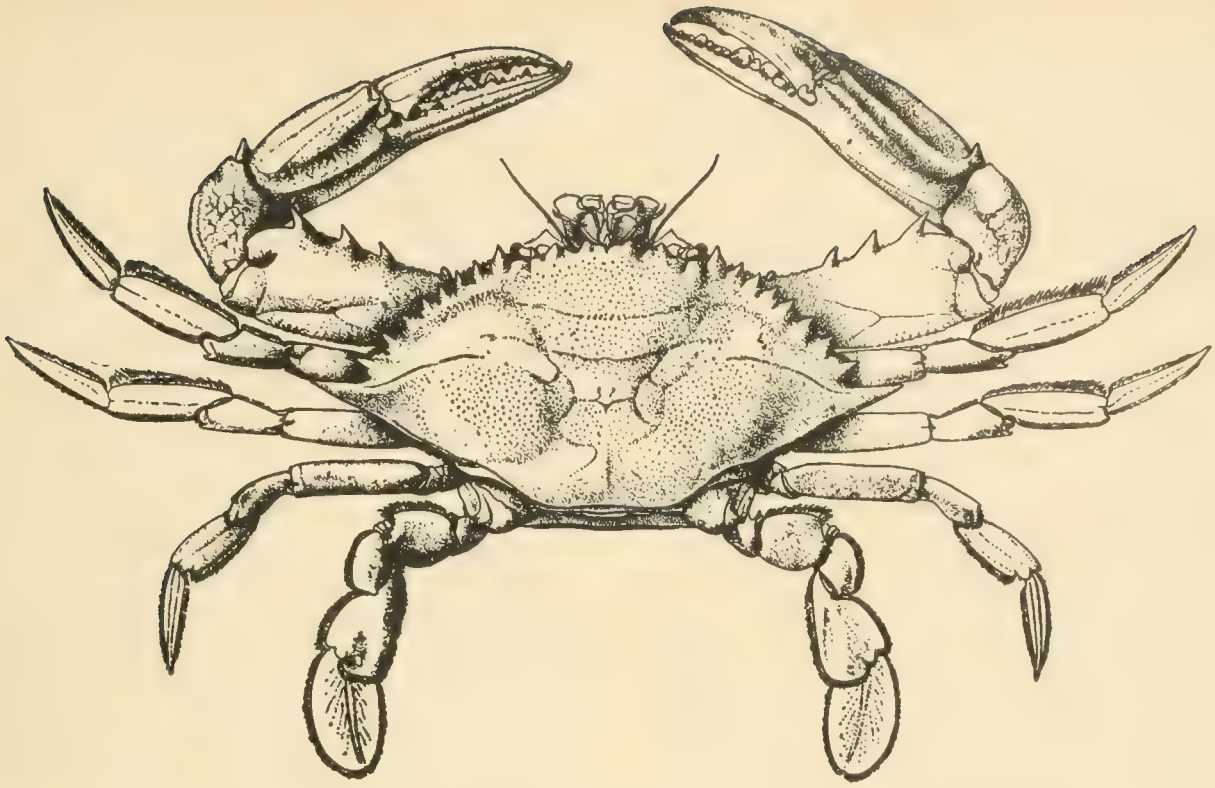

FIGURE 151.—*Callinectes sapidus* Rathbun. Animal in dorsal view (after Rathbun, 1884).

Habitat.—Found on a variety of bottom types in estuaries and shallow oceanic water; water's edge to 20 fathoms.

Type locality.—[East coast of United States].

Known range.—Native recent range, Nova Scotia (no longer endemic, Bousfield, personal communication) to Uruguay; Bermuda. The species has been introduced in Europe, and was reported from southwest France in 1901; from Holland in 1932, 1934, and 1951; near Copenhagen, Denmark, in 1951; in and near Venice, Italy, in 1949 and 1950; and in Israel in 1955. Holthuis (1961) reviewed these occurrences in addition to recently found well-established colonies in Turkey and Greece and remarked that the species must now be regarded as indigenous to Europe.

Remarks.—There is a tremendous literature concerning the blue crab, largely because of its great economic value. Since it is not possible to summarize this literature in a brief account such as this, the interested student is referred to the comprehensive bibliography compiled by Cronin, Van Engel, Cargo, and Wojcik (1957) for a list of the literature to that date, to excellent life history and ecological summaries by Churchill (1919), Truitt (1939), and Van Engel (1958) for the crab in Chesapeake Bay; and to Darnell (1959) for occurrence in Louisiana. Though these papers are current and available, for the sake of convenience certain essentials are reviewed here.

The fossil record for *Callinectes sapidus* reaches back to the lower Miocene of Florida, and the species has been found at later levels in Virginia, Massachusetts, New Jersey, and the Carolinas (Rathbun, 1935; Blake, 1953).

The spawning season on the east coast of the United States is quite long. Females with yellow egg masses attached have been found in North Carolina from as early as March 21 to as late as October 26. In that area, the greatest number of females with eggs occur in spring, the time of peak occurrence varying somewhat with season. In Chesapeake Bay, the spawning season, with rare exceptions, extends from late April to early September with the peak occurring in June. Farther south, on the coast of Texas the spawning season extends from December to October and may include November as well, but the peak oc-

curs in June and early July (Daugherty, 1952). Five stages in the reproductive cycle of mature females have been described (Hard, 1942), and a number of authors have shown that the number of eggs in an egg mass (sponge) may range from 700,000 to more than 2 million.

The eggs hatch into zoeae, undergoing development through seven stages. These stages have been described from laboratory cultures (Costlow, Rees, and Bookhout, 1959; Costlow and Bookhout, 1959). Atypically, an eighth stage may occur. The last zoeal stage molts into a megalops stage and this into the first crab stage.

Churchill found that eggs hatch in about 15 days at 26.1° C. and slightly faster at higher temperatures. Development from hatching to megalops lasts from 31 to a maximum of 49 days in various salinities, but development time in the different stages is quite variable even in a single salinity-temperature combination. The megalops stage lasts from 6 to 20 days. It was found that development progresses at a comparable rate in salinities between 20.1 and 31.1 °/₀₀ at 25° C. Salinity above 31.1 °/₀₀ slowed development, and below 20.1 °/₀₀ larvae rarely completed the first molt. Larvae never went beyond the first zoeal stage when reared at 20° C. and did not progress beyond the third zoeal stage when reared at 30° C. Once the first crab stage is reached, the animals continue to molt as they grow and are estimated to undergo some 18 to 20 or more molts before reaching maturity (Van Engel, 1958).

In Chesapeake Bay, where the crab is perhaps more abundant than in other areas, it has been demonstrated that crabs spawned in June of one year are mature about 14 months later and at that time mate. Most mating pairs are found in July, August, or September, though the mating season extends from May to October. At this time, females ready to molt into the mature stage (terminal molt) are carried about, cradled upright, under the males' bodies. Such pairs are called doublers. The male frees the female during the time she is actually casting the old exoskeleton, but when this is shed he grasps her again, this time with the ventral surfaces together, and completes the breeding act by introducing sperm via the copulatory stylets into the spermathecae. Copulation may last for several hours. When sperm transfer is complete, the female is allowed to resume an upright posture and is again carried under the male for a time until her shell is hardened. Males may mate more than once and at any time during their last three intermolts (Van Engel, 1958); females only do so once, but the sperm supply may serve to fertilize more than one mass of eggs. Usually, a female mated in late summer casts the first batch of eggs the following spring at an age of approximately 2 years, but egg laying may be at any time from 2 to 9 months after mating. A second spawning has been observed to occur later in summer among some individuals, and it is possible that a third may occur, possibly as late as the succeeding spring or at an age of 3 years. Three years is judged to be about the normal maximum age for this species.

The life history of the blue crab is complicated by the fact that it leads a migratory existence. The migratory patterns have been studied in greatest detail in Chesapeake Bay but the same pattern appears to be true of other areas as well. Mating usually takes place in water of reduced salinity well up in estuaries. After this, the females migrate downstream to areas of higher salinity near the mouths of estuaries where the eggs are laid and hatched, whereas the males tend to remain in the low-salinity areas for the remainder of their lives. For this reason, samples of adult crabs (or commercial catches) near the sea contain greater numbers of females, whereas those from the middle or upper reaches of bays contain larger percentages of males except at the breeding season. Once in the spawning areas, the females tend to remain there for the remainder of their lives or move a short way out to sea. Once hatched, the zoeae lead a planktonic existence until they transform to the megalops stage. As soon as the crabs transform to the first crab stage, they begin a migration up the estuary toward the mating grounds. Some early recruits may reach these areas in their first summer of life, the remainder early in the second year of life. In areas smaller than Chesapeake Bay, there may be a certain amount of overlap in mating and spawning grounds but the two areas tend to be distinct. In Chesapeake Bay, the spawning grounds are near the mouth of the Bay; in North Carolina and Louisiana, near the inlets and passes. In Texas,

most females with eggs are found in the Gulf proper (Daugherty, 1952).

Aside from size variation associated with the annual growth cycle, there is an apparent variation in size correlated with location in which the animals are found (Van Engel, 1958). Though never conclusively proved by experiments, it is thought that there is a negative correlation of size with the salinity in which a crab matures. Very large males are probably large because they have remained in water of low salinity. Fischler (1959) reviewed the occurrence of "dwarf" ovigerous females ranging in width from 52.3 to 80 mm. All these specimens were taken near the sea, and, as the author pointed out, may be small because of environmental influences of high salinities throughout life.

That the blue crab can tolerate fresh water is well established. The subject is reviewed in some detail by Odum (1953). On the basis of experiment and observation he reached the conclusion that oligohaline (100–1,000 p.p.m. Cl) and nearly oligohaline waters (25–100 p.p.m. Cl) can be invaded to a considerable extent if the crabs are able to adjust slowly to the reduced chlorinity, which, of course, is the case in natural invasions. Many of the Florida streams and lakes are oligohaline and contain blue crabs, but in other areas this is not true and blue crabs in such areas are seldom found far from salt water.

Because the blue crab supports the largest crab fishery in the United States, fluctuations in abundance (especially in the Chesapeake area) have been the subject of many conjectures and a number of investigations. Pearson (1948) dealt with this subject at length. The fluctuations appear to be associated with variable rates of survival in the first year of life. No correlation was found between relative abundance of female crabs and their progeny. On the basis of examination of 13 generations, size of spawning stock did not determine size of population surviving to commercial age at the rate of fishing prevailing during the years studied. Pearson found evidence that excessively cold weather may reduce availability of immature and adult crabs either by direct mortality or by making crabs less available to the fishery immediately after the periods of cold weather. Heavy runoff in some wet years may lower salinity in the spawning areas enough to have an adverse effect on survival of young, but such limits are poorly understood.

Piers (1923) reported a population of blue crabs in Nova Scotia, the recorded northern limit for the species, and considered that it was a natural rather than an introduced population. Bousfield (personal communication) reports that the species is certainly no longer endemic there. Scattergood (1960) commented that fluctuations in the population in Maine seemingly were correlated with temperature when a series of warm years accompanied an increase in number of blue crabs.

The blue crab is often summarily dismissed as a scavenger. Though it may be a scavenger, and, indeed, is lured to crab pots or wire traps by means of dead fish used for bait, students of the feeding habits of the species agree that it is an omnivore and prefers fresh to putrid flesh (Churchill, 1919; Truitt, 1939; Van Engel, 1958). Darnell (1961) showed that blue crabs in Lake Pontchartrain, La., eat a variety of materials including fishes, large and small bottom animals, some vascular plant material, and organic detritus. Of these materials, the category including small bottom animals (*e.g.*, those that are intimately associated with the bottom) made up about half of the diet. There are numerous notes on feeding and predation in the literature recording such habits as feeding on oysters, clams, and tunicates.

In a study of gill area correlated with degree of activity and habit of several species of crabs, Gray (1957) found that the blue crab has a larger gill area per gram of body weight than the other portunids studied (*Ovalipes*, *Arenaeus*, and *Portunus* spp.) and, in fact, exceeded that of any crab studied among aquatic, intertidal, and land crabs in the Beaufort, N.C., area. The blue crab is noted for its vigorous and pugnacious nature, and this anatomical feature gives one reason for such temperament.

Callinectes sapidus is fairly long-lived following its last molt, and thus affords a lodging place for barnacles and bryozoans. Its gills and gill chambers become clogged with clusters of a small stalked barnacle, *Octolasmus lowei* (Causey, 1961). The barnacles *Balanus amphitrite* and *Chelonibia patula* attach to the carapace. The sacculinid parasite, *Loxothylacus texanus*, lives

beneath the abdomen (Wass, 1955). Hopkins (1947) discussed infestations of the parasitic nemertean *Carcinonemertes carcinophila* on female blue crabs showing that only light-colored worms are found in the gills of mature females which have never spawned. Large red worms are found only on the gills of mature female crabs which have spawned at least once, or in the gills and egg masses of ovigerous females. Presence of large red nemerteans in the gills is a sure sign that the crab has spawned some time in the past. Pearse (1932b) reported trematode metacercariae on the gills.

Pigment in the melanophores of *C. sapidus* displays an endogenous rhythm with a frequency of 24 hours in the Gulf of Mexico where there is one high and one low tide per day (Fingerman, 1955). The pigment is in a dispersed state during the day and in a contracted state at night. This cycle is maintained under constant laboratory conditions. Superimposed on the diurnal rhythm is a tidal rhythm with a frequency of 12.4 hours. This rhythm is manifested by a supplementary dispersion of melanin which occurs about 50 minutes later each day and is most evident when the low or high tide is either in the morning or late afternoon. Under constant conditions, the phases bear a definite relationship to times of low and high tides in the native habitat. Also, there is evidence for a semilunar rhythm. Only once every 14.8 days are the diurnal and tidal rhythms in the same phases relative to each other.

Callinectes ornatus Ordway

Figure 152

Callinectes ornatus Ordway, 1863, p. 571.—Hay and Shore, 1918, p. 433, pl. 34, fig. 2.—Rathbun, 1930a, p. 114, pl. 50 (rev.).

Recognition characters.—Carapace, including lateral spines, slightly more than twice as wide as long, somewhat tumid, finely granulate throughout, transverse lines distinct, metagastric area less than half as long as its anterior width. Six frontal teeth including inner orbitals, submedial teeth short, variable in length. Anterolateral teeth shallow and broad, tips of first five or six acute, others acuminate; lateral spines curved forward, scarcely as long as space occupied by three preceding teeth; inner suborbital angle prominent.

Chelipeds shaped as in *C. sapidus*, but smaller, with spines possibly more acute; ridges of hand

FIGURE 152.—*Callinectes ornatus* Ordway. Animal in dorsal view, legs not shown, 10 mm. indicated.

more developed, and teeth on fingers relatively larger and sharper. Abdomen of male with first segment produced laterally into an acute, upturned spine.

Measurements.—Carapace: male, length, 33 mm.; width, 74 mm.

Color.—Adult male: Carapace green dorsally, irregular areas of iridescence at bases of, and between, anterolateral teeth, and on posterior and posterolateral borders. Chelipeds and portions of legs similar in color or more tannish green dorsally, with iridescent areas on outer and upper edges of carpus and hands; chelae white on outer face, blue to fuchsia on inner surface, with fuchsia on tips of fingers and teeth of opposed edges. Lateral spines and some anterolateral teeth, as well as spines on chelipeds, white tipped. Walking legs grading from fuchsia distally through violet blue to light blue mottled with white proximally, pubescence on legs beige. Swimming legs variably mottled with white; all legs with stellate fuchsia markings at articulations. Under parts white and blue.

Ovigerous female: similar to male except with more violet blue on inner surface of chelae; fingers either with white teeth or fuchsia-colored teeth. Legs with dactyls reddish orange grading abruptly to blue on propodi, pubescence brown to beige. Abdomen with iridescent areas.

Habitat.—This crab, like its near relative, *C. sapidus*, is a coastal species often found in estuaries, sometimes in fresh water. Brues (1927) observed a large, active male that had been trapped at the head of a Cuban tidal river in fresh water during a dry period of about 3 months' duration. Lunz (1958), writing of a form from the South Carolina crab fishery,

doubtfully referred to *C. ornatus*, said that it tends to occupy oceanic waters and high- to medium-salinity areas of estuaries chiefly in a temperature range of 15° to 31° C., but has been found in temperatures as low as 9° C. From over 500 trawl hauls in South Carolina, a depth maximum of 9 fathoms was found for the species. However, specimens have been taken under a light at night swimming at the surface in 925-fathom water off the Mississippi River Delta (U.S. National Museum notes).

Reported from surface to 40 fathoms, with above exception.

Type localities.—Charleston Harbor [S.C.]; Tortugas [Fla.]; Bahama Islands; Gonaives [Haiti]; Cumana [Venezuela].

Known range.—New Jersey to State of São Paulo, Brazil; Bermuda.

Remarks.—Blake (1953) reported a fossil record for this species dating from the Pleistocene of Maryland. Lunz (1958), in addition to habitat data, reported ovigerous females from South Carolina in May, August, and September, and added that spawning probably takes place offshore. He found a sex ratio of approximately two males to one female. Ovigerous females occur as late as November in North Carolina.

Genus *Arenaeus* Dana, 1851

Rathbun, 1930a, p. 134.—Hemming, 1958b, p. 13.

Arenaeus cribrarius (Lamarck). Speckled crab

Figure 153

Portunus cribrarius Lamarck, 1818, p. 259.
Arenaeus cribrarius: Hay and Shore, 1918, p. 434, pl. 34, fig. 3.—Rathbun, 1930a, p. 134, pl. 58, figs. 2–3; pls. 59–60 (rev.).

Recognition characters.—Carapace more than twice as wide as long, finely granulate, produced on each side into a strong spine. Front not so far advanced as outer orbital angles, with six teeth including inner orbitals; central tooth of each side partly coalesced with adjacent submedian tooth. Anterolateral teeth strong, somewhat acuminate, heavily ciliate beneath. Superior wall of orbit with two deep fissures dividing it into three lobes; inferior wall of orbit with wide external fissure and inner angle much advanced; lower surface of carapace hairy.

Chelipeds of moderate size; merus with three spines on anterior border, and a short tuberculiform one near distal end of posterior border; carpus with two spines; hand short, with five longitudinal granulose ridges and two spines, one at articulation with carpus, another above base of dactyl. Walking legs rather short and broad, densely ciliate. Swiming legs stout. Basal segment of abdomen produced on each side into strong, sharp, slightly upcurved spine.

Measurements.—Carapace: male, length, 48 mm,; width, 116 mm.

Color.—Light vinaceous brown or olive brown thickly covered over dorsal surface with small, rounded, white spots; spots on dorsal surface of chelipeds somewhat larger; tips of walking legs yellow. Color pattern persisting in alcohol.

Habitat.—As far as known, this crab seldom enters estuaries and is rarely washed ashore along the outer beaches. It lives in rather shallow water close to the shore, and is well adapted to life in the waves and shifting sand. Hildebrand (1954) reported it as preferring the relatively shallow water of the white shrimp grounds in Texas. Siebenaler (1952) reported it as a "trash" form on the Florida east coast shrimp grounds. Waterline along beaches to 37 fathoms.

Type locality.—Brazil.

Known range.—Vineyard Sound, Mass., to State of Santa Catarina, Brazil.

Remarks.—Ovigerous females are known in August from Florida, and in September from Venezuela and Brazil.

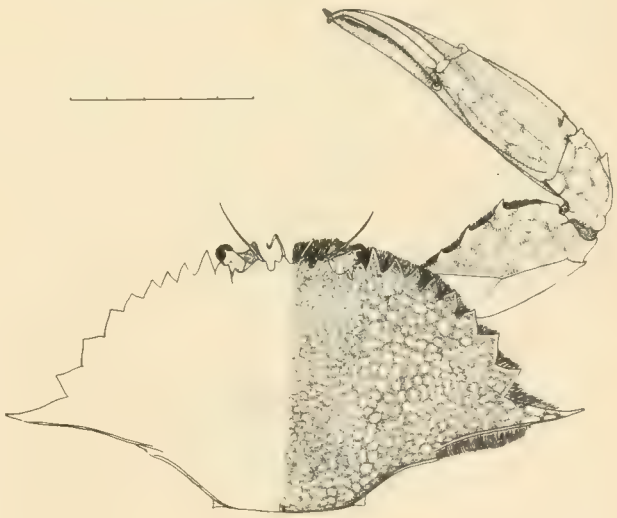

FIGURE 153.—*Arenaeus cribrarius* (Lamarck). Male in dorsal view, legs not shown except for right cheliped, color pattern of right side indicated, 50 mm. indicated.

Pearse, Humm, and Wharton (1942) stated that where waves roll at the low-tide mark *A. cribrarius* may scurry across sand and burrow backward. In doing this, the crab flirts sand forward away from the body with the chelipeds, waves legs two to four rapidly from the median line laterally, and moves the fifth legs posteriorly and dorsally, thus sinking vertically into the sand. Often the crabs bury themselves completely. The heavy coat of hairlike setae on each side of the mouth parts keeps out sand, and with the chelipeds held close to the body a clear channel is left for currents from the branchial chamber. Ability to maintain strenuous activity in the breaker zone near shore may be partially explained also by the relatively large respiratory surface in this species (Gray, 1957).

Genus ***Cronius*** Stimpson, 1860

Rathbun, 1930a, p. 138.

Cronius ruber (Lamarck)

Figure 154

Portunus ruber Lamarck, 1818, p. 260.
Cronius ruber: Rathbun, 1930a, p. 139, pls. 62–63 (rev.).

Recognition characters.—Carapace hexagonal, smooth, pubescent; a sinuous transverse ridge extending between lateral spines, and another shorter, transverse, biarcuate ridge about halfway between this ridge and front. Front proper with four teeth, not including inner orbitals; submedian pair of teeth most advanced; second pair more pointed, and directed slightly laterad, separated from notched inner orbitals by a deep cut. Orbit nearly circular. Basal article of antenna with spine below insertion of movable portion. Anterolateral teeth unequal, alternating large and small; lateral spine not strikingly enlarged.

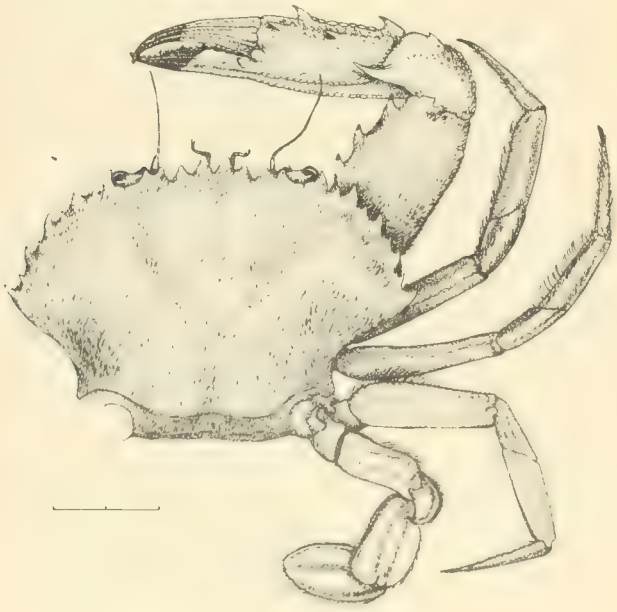

FIGURE 154.—*Cronius ruber* (Lamarck). Animal in dorsal view, legs of left side not shown; (redrawn from Monod, 1956).

Chelipeds heavy; merus with four to six spines in front, and with small distal spine behind; carpus with granulate ridges, one large internal spine, and three small spines on outer surface; hand with granulate ridges on all surfaces, armed with four spines on superior surface, two on inner and two on outer border.

Measurements.—Carapace: male, length, 50 mm.; width, 75 mm.

Color.—"Violet red or deep purple red more or less marbled with a lighter shade or white. Extremity of all spines black." (Rathbun, 1930a.)

Habitat.—Siebenaler (1952) reported *C. ruber* as a "trash" form on the Tortugas shrimping grounds; below low tide mark to 40 fathoms.

Type locality.—Brazil.

Known range.—South Carolina to State of Santa Catarina, Brazil; Lower California, Mexico, to Peru and Galapagos Islands; west Africa from Senegal to Angola.

Remarks.—Rathbun (1930a) reported ovigerous females from May through September in Curaçao, in June from Cuba, and in July from Jamaica.

Family **Cancridae**

Carapace broadly oval or hexagonal. Last pair of legs not adapted for swimming. Antennules folding lengthwise. Antennae with flagella more or less hairy.

Genus ***Cancer*** Linnaeus, 1758

Rathbun, 1930a, p. 176.—Hemming, 1958b, p. 51.

MacKay (1943) gave a review of the modern world distribution of members of the genus *Cancer*, as well as the geologic record which dates from the Eocene Period. The modern distribution of the genus is limited, apparently by temperature, to the temperate zones except along the northwestern coast of South America in the cold Humboldt Current.

KEY TO SPECIES IN THE CAROLINAS

a. Anterolateral teeth of carapace with margins granulate; chelipeds granulate, not denticulate
irroratus (p. 175).

aa. Anterolateral teeth of carapace with denticulate margins; upper margin of palm denticulate
borealis (p. 175).

Cancer irroratus Say. Rock crab

Figure 155

Cancer irroratus Say (in part), 1817, p. 59, pl. 4, fig. 2.—Hay and Shore, 1918, p. 435, pl. 35, fig. 1.—Rathbun, 1930a, p. 180, text-fig. 29, pl. 85, fig. 1 (rev.).

Recognition characters.—Carapace approximately two-thirds as long as wide, convex, granulated. Anterolateral border divided into nine teeth with margins granulate, not denticulate as in *C. borealis*, and with notches between teeth continued on carapace as short, closed fissures giving teeth a pentagonal character. Posterolateral border a granulated ridge with one tooth at outer end similar to those of anterolateral border but smaller. Front with three teeth, middle one exceeding others and depressed.

Chelipeds of moderate size, not so long as second pair of legs; carpus with granulated ridges and a sharp spine at inner distal angle; hand nearly smooth on inner face, outer face with four or five granulated lines, two lower ones continued on slightly deflexed immovable finger, superior one cristate. Walking legs rather long and slender; merus of first and second pairs extending far beyond carapace. Abdomen of male broad, first, second, and third segments with transverse granulated ridge.

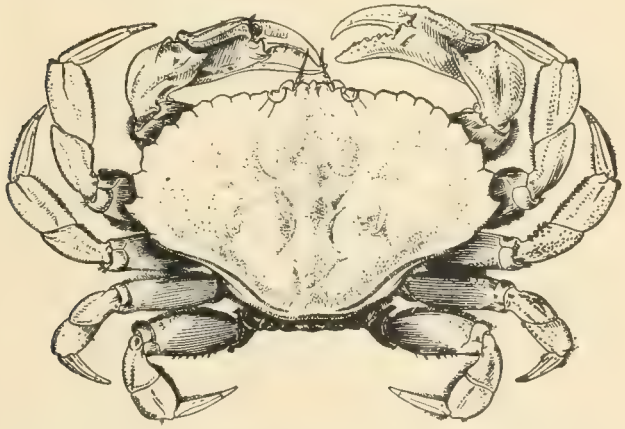

FIGURE 155.—*Cancer irroratus* Say. Male in dorsal view, reduced (after Rathbun, 1884).

Measurements.—Carapace: length, 65 mm.; width, 95 mm.

Color.—Yellowish closely dotted with dark purplish brown, becoming reddish brown after death.

Habitat.—Most individuals taken near Beaufort, N.C., are immature, but larger specimens have been taken farther from the coast. This species, and the following one, are members of a northern fauna with ranges extending south of the Carolinas only in deep water. Low water mark to 314 fathoms.

Type locality.—"Inhabits the ocean." [Atlantic coast of United States.]

Known range.—Labrador to South Carolina; shallow water in the North, deeper water in the South.

Remarks.—This species has a fossil record extending from the Miocene to the present in North America (MacKay, 1943). Ovigerous females are known to occur in March in Florida, and have been reported in August from Massachusetts (Rathbun, 1930a).

Cancer borealis Stimpson. Jonah crab; northern crab

Figure 156

Cancer borealis Stimpson, 1859, p. 50.—Hay and Shore, 1918, p. 434, pl. 35, fig. 2.—Rathbun, 1930a, p. 182, text-fig. 30 (rev.).

Recognition characters.—Carapace transversely oblong, approximately two-thirds as long as wide, angular at sides, surface granulate. Anterolateral margins divided into nine quadrangular, crenate lobes or teeth, with margins minutely denticulate and with notches between teeth continued on carapace as short closed fissures. Front produced beyond internal orbital teeth and provided with three teeth, center one longest and depressed. Orbits circular, with two narrow fissures above and two below; suborbital lobe strongly produced.

Chelipeds nearly as long as second pair of legs, stout; carpus and hand with strong, granulose rugae; carpus with sharp spine at inner angle; hand smooth on inner face, heavily rugose on outer face, two rugae continued from hand on slightly deflexed immovable finger; dactyl with rough upper surface, both fingers slaty black at tip. Walking legs short, fringed beneath, dactyls dark tipped.

Measurements.—Carapace: length, 62 mm.; width, 91 mm.

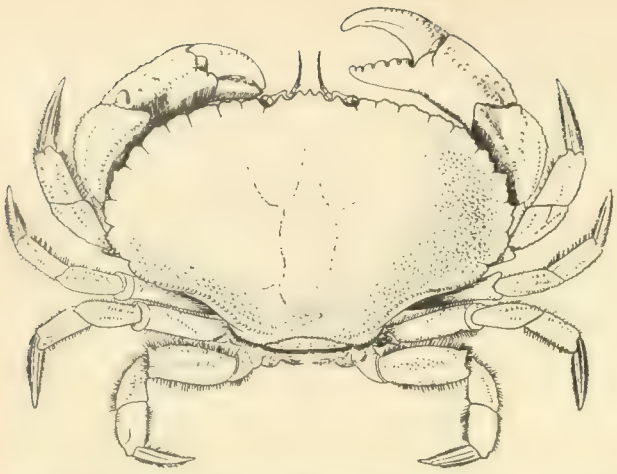

FIGURE 156.—*Cancer borealis* Stimpson. Male in dorsal view, reduced (after Smith, 1879).

Color.—Yellowish beneath, red above; back with two curved lines of yellowish spots and, behind middle, a figure somewhat resembling letter H; legs mottled and reticulated with yellow and red, more or less purplish.

Habitat.—Small and immature individuals are found in the Beaufort, N.C., harbor region; larger individuals occur in deep water off the coast; between tides among rocks to 435 fathoms.

Type localities.—Nova Scotia to Cape Cod.

Known range.—Nova Scotia to south of Tortugas, Fla.; Bermuda.

Remarks.—This species has a fossil record dating from the Miocene of North America (MacKay, 1943). Ovigerous females are recorded in June from southern Florida.

Family **Xanthidae**

Crabs with body transversely oval or transversely hexagonal. Front broad, never produced in form of a rostrum. Last pair of legs normal. Antennules folding obliquely or transversely. Male openings rarely sternal (Rathbun, 1930a).

In the key to the genera of Xanthidae in the Carolinas it has been impossible to use characters which show the general relationships unless pleopods of the males are employed. Differences between genera are often subtle and the general worker is, therefore, compelled to use a combination of trivial characters for identification. Because most of the genera occurring in the Carolinas contain a single species, the generic key is in large part also a key to species. Parts of the key have been adapted from Rathbun (1930a) and Ryan (1956).

Arrangement of the genera differs in some respects from that of Rathbun and is based on similarities and differences in the first pair of male pleopods. In such arrangement I follow broadly the arrangements of Stephensen (1945) and Monod (1956). As in Rathbun (1930a) and Monod (1956), no attempt is made to divide the family Xanthidae into subfamilies, though at least three well-marked groups appear in the Carolinas, and perhaps the third of these groups (fig. 183) could be split into additional groups.

KEY TO GENERA IN THE CAROLINAS

a. Entire body and legs with surface deeply and intricately eroded, resembling piece of stony coral.—*Glyptoxanthus* (p. 185).
aa. Entire body and legs with surface not deeply and intricately eroded.
  b. Antennae widely separated from orbits.—*Eriphia* (p. 182).
  bb. Antennae not separated from orbits.
    c. Chelipeds with a large notch clearly forming an open hole between carpus and hand when viewed frontally with chelipeds fully pressed against body.—*Carpoporus* (p. 186).
    cc. Chelipeds without a large notch clearly forming an open hole between carpus and hand when viewed frontally with chelipeds fully pressed against body.
      d. Extreme edge of frontal margin with shallow transverse groove, each half appearing double (under magnification).
        e. Carapace more or less nodose in front, upper edge of frontal groove formed by line of nodules.—*Leptodius* (p. 192).
        ee. Carapace not nodose in front but with transverse ridges on dorsum.—*Rhithropanopeus* (p. 187).
      dd. Extreme edge of frontal margin not transversely grooved, each half presenting but a single edge (under magnification).
        e. Teeth of anterolateral border subtriangular or with edges flattened and rounded; carapace never nodose.
          f. Carapace with regions on dorsum defined; carapace not smooth to unaided eye.
            g. Major cheliped with a more or less conspicuous tooth at base of dactyl, tooth larger than adjacent teeth and often of contrasting color.

h. Third and fourth teeth of anterolateral border definitely pointed forward with outer borders curved.
i. Tooth at base of major dactyl large and conspicuous; body definitely arched above—*Panopeus* (p. 196).
ii. Tooth at base of major dactyl present but often not large and conspicuous; posterior two-thirds of carapace flattened above—*Eurypanopeus* (p. 194).
hh. Third and fourth teeth of anterolateral border triangular and pointing outward or slightly forward, outer borders not conspicuously curved—*Hexapanopeus* (p. 188).
gg. Major cheliped with no tooth at base of dactyl, or with obsolescent tooth little if any larger than adjacent teeth.
h. A red spot on internal face of ischium of third maxillipeds—*Eurypanopeus* (p. 194).
hh. No red spot on internal face of ischium of third maxillipeds—*Neopanope* (p. 190).
ff. Carapace with regions on dorsum obsolete; carapace smooth to unaided eye.
g. Fingers white; anterolateral teeth pointed or rounded—*Eurytium* (p. 199).
gg. Fingers black; anterolateral teeth broad, not pointed, with occasional exception of most lateral tooth; often attains large size—*Menippe* (p. 183).
ee. Teeth of anterolateral border usually distinctly spiny or spiniform; sometimes subtriangular, serrated or with spiny tips, and with carapace more or less nodose (nodes occasionally small).
f. Carapace nearly devoid of hairs and with nodose areas on front and anterolateral portions usually clearly evident, though sometimes poorly developed; adult size small—*Micropanope* (p. 192).
ff. Carapace with either long, plumose hairs, numerous short hairs, or both.
g. Carapace and chelipeds variably spiny; not nodose; with long plumose (clubbed) hairs, short hairs, or both—*Pilumnus* (p. 177).
gg. Carapace with patches of nodules on anterolateral margins extending back from front; with close pile of short hair only; body massive, thick—*Lobopilumnus* (p. 181).

Genus *Pilumnus* Leach, 1815

Rathbun, 1930a, p. 481.—Hemming, 1958b, p. 35.

KEY TO SPECIES IN THE CAROLINAS

a. Hair not covering whole carapace or not forming so thick a coat as to conceal surface beneath.
b. Two or more superhepatic spines—*sayi* (p. 177).
bb. No superhepatic spines—*dasypodus* (p. 178).
aa. Hair covering whole carapace and forming a thick coat concealing surface beneath (hair sometimes worn off).
b. Chelipeds spinose above; a transverse row of long hairs across front—*floridanus* (p. 179).
bb. Chelipeds not spinose above; carapace tuberculate, but tubercles often sparse and low.
c. Tubercles of carapace not numerous nor prominent, upper margin of orbit not spinose—*lacteus* (p. 180).
cc. Tubercles on anterior half of carapace and upper surface of chelipeds numerous, upper margin of orbit with truncate spines (but occasionally these poorly developed)—*pannosus* (p. 181).

Pilumnus sayi Rathbun. Hairy crab

Figures 157 A, B; 158

Cancer aculeatus Say, 1818, p. 449.
Pilumnus sayi Rathbun: 1897b, p. 15.—Hay and Shore, 1918, p. 440, pl. 35, fig. 4.—Rathbun, 1930a, p. 484, pl. 200, figs. 1–2; pl. 201, figs. 4–7 (rev.).

Recognition characters.—Carapace about three-fourths as long as wide, anterior half semicircular, strongly deflexed, sparsely covered with long filiform and plumose hairs. Anterolateral border with four marginal spines including outer orbital; two curved spines on hepatic region with sometimes one, two, or three supplementary spines; one long spine and sometimes spiniform tubercles between first and second marginal spines below margin. Orbit armed with three long spines above, and four long and two to four short spines below. Front advanced, deeply notched in center, less so on each side, armed with about four spines on each side.

Superior surfaces of chelipeds and walking legs with many filiform and plumose hairs; carpal and propodal articles most thickly covered and with several strong spines as well. Chelipeds large, unequal; carpus with 15 or 20 erect dark spines; spines of hand strong and acute above but becoming smaller on external surface, spines tending to arrangement in rows on large hand; fingers ribbed, dark, and with obtuse teeth; dactyl spiny above at base.

Measurements.—Carapace: male, length, 23 mm.; width, 32 mm.

Variations.—The specimen taken on Frying Pan Shoal off North Carolina (Charleston Museum No. 38.228) reported by Lunz (1939) appears to be an aberrant specimen of *Pilumnus sayi* rather than *P. marshi.* The specimen lacks superhepatic spines on the carapace but otherwise more nearly resembles *P. sayi* than any other Western Atlantic species of *Pilumnus.*

Color.—Grayish brown irregularly suffused with red or purple on body and legs; spines black, horn color, or purple; fingers of chelae black or brownish purple.

Habitat.—This species is fairly common in the Carolinas, and is often taken on shelly bottom. It has been taken from wharf piles, buoys (Lunz, 1937a), the sponge *Stematumenia strobilina* (Lamarck) (Pearse, 1934), and from offshore reefs (Pearse and Williams, 1951). From low-water mark to 49 fathoms.

Type locality.—Georgia and east Florida.

Known range.—North Carolina through Gulf of Mexico and West Indies to Curaçao.

Remarks.—Ovigerous females occur in the Carolinas from May to August, and as early as March in Florida (Wass, 1955). Chamberlain (1961) reported four zoeal stages and one megalops stage in the larval development of the species,

FIGURE 157.—Male first pleopods in medial view; A, *Pilumnus sayi* Rathbun, entire pleopod; B, *Pilumnus sayi* Rathbun, tip in detail; C, *Pilumnus dasypodus* Kingsley, tip; D, *Pilumnus floridanus* Stimpson, tip; E, *Pilumnus lacteus* Stimpson, tip; F, *Pilumnus pannosus* Rathbun, tip; G, *Lobopilumnus agassizii* (Stimpson), tip; 0.125 mm. indicated.

FIGURE 158.—*Pilumnus sayi* Rathbun. A, male in dorsal view, walking legs of left side not shown, 10 mm. indicated; B, large chela in frontal view, 10 mm. indicated.

but did not describe the stages in detail. He found that larval development time varied with temperature (18 days at 30° C., 28 at 21° C.) and with food. Larvae matured most rapidly when fed *Artemia salina* nauplii, did moderately well on *Artemia* and algae, but did not transform at all when fed algae alone.

Pilumnus dasypodus Kingsley

Figures 157C, 159

Pilumnus dasypodus Kingsley, 1879, p. 155.—Rathbun, 1930a, p. 493, pl. 200, figs. 5–6 (rev.).

Recognition characters.—Carapace thinly covered on anterior two-thirds with long, fine hair and occasional stouter setae; upper surface of chelipeds and walking legs similarly clothed; small sharp granules on anterolateral region. Anterolateral border with four spines including small outer orbital; spines with bases conical, extremities long, slender, incurved. Orbital border with three or four spines above and about seven below. Frontal lobes separated by a

median V- or U-shaped notch; margins furnished with short spines or sharp granules, with an outer tooth separated from remainder of margin by a U-shaped notch.

Chelipeds unequal, spinose, and granulate except for smooth and naked lower distal two-thirds of outer surface of major palm, spines and granules not arranged in rows on upper part of major palm; fingers of minor chela grooved on outside, dactyls with rows of sharp granules and hairs at base. Walking legs spinose above.

Measurements.—Carapace: male, length, 11 mm.; width, 15 mm.

Color.—Body and claws brownish-red color, legs much lighter; fingers and extremities of spines brown (Milne Edwards *in* Rathbun, 1930a).

Habitat.—This species has been taken from pilings, jetties, and buoys (Lunz, 1937a), and from offshore reefs (Pearse and Williams, 1951) in the Carolinas; and from similar situations elsewhere (Rathbun, 1930a) including loggerhead sponge *Speciospongia vespara* (Lamarck) (Pearse, 1934). One-half to 16 fathoms.

Type locality.—Key West, Fla.

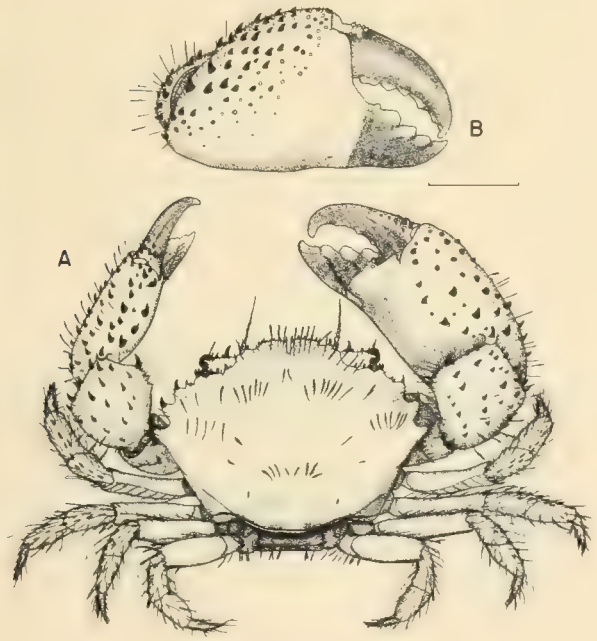

FIGURE 159.—*Pilumnus dasypodus* Kingsley. A, male in dorsal view; B, large chela in frontal view; 5 mm. indicated.

Known range.—Off Cape Hatteras, N.C., through Gulf of Mexico and West Indies to State of Santa Catarina, Brazil.

Remarks.—This species is not so common in the Carolinas as *P. sayi*, and small specimens of *dasypodus* are not always easily distinguished from *sayi*. Rathbun (1930a) stated that, "*dasypodus* is less heavily clothed with hair than *sayi* and less ragged looking. The front is more deflexed and less advanced, therefore appears wider. The spines and tubercles of the major palm in *sayi* are arranged more or less in rows and these rows have a tendency to encroach on the lower distal half; in *dasypodus* there are seldom any definite rows and the lower distal two-thirds or one-half in both sexes is smooth and bare. The immovable finger of the major chela in *dasypodus* is a little longer than in *sayi*."

Lunz (1937a) reported ovigerous females from April through August in the Carolinas, and they have been found in North Carolina in September. In the West Indies they occur at all seasons of the year (U.S. National Museum records).

Pilumnus floridanus Stimpson

Figures 157D, 160

Pilumnus floridanus Stimpson, 1871a, p. 141.—Rathbun, 1930a, p. 507, pl. 205, figs. 3–4 (rev.).

Recognition characters.—Carapace covered with dense, short pubescence thinning behind, and with a few longer clavate hairs, a conspicuous transverse series of these crossing frontal region. Anterolateral margin with four somewhat conical spines; a small subhepatic spine between outer orbital and second spine; hepatic region slightly roughened but with no spines. Frontal lobes almost bare, edge slightly oblique, entire, with median triangular notch and rounded lateral notches; tooth at outer angle minute, deflexed. Orbital margin unarmed above, with 8 to 10 spinules below.

Chelipeds spinose above; merus with two spines near distal end on upper surface; carpus armed over entire exposed surface; spines on hand becoming pointed tubercles on outer surface. Male with large hand smooth and bare on outer lower half or less of surface, smooth portion more restricted in female. Walking legs spined above.

Measurements.—A small species. Carapace: male, length, 7 mm.; width, 10 mm.

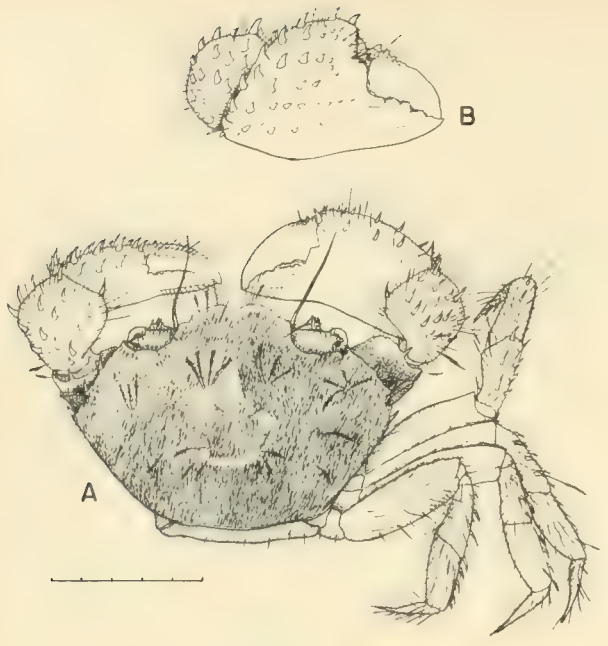

FIGURE 160.—*Pilumnus floridanus* Stimpson. A, animal in dorsal view, walking legs of left side not shown; B, large chela in frontal view; 5 mm. indicated.

Habitat.—In North Carolina this species has been taken from an offshore reef (Pearse and Williams, 1951) and has been found in sponges. Rathbun (1930a) listed it as taken from rocks, grass, and a variety of bottoms. Low-tide mark to about 80 fathoms.

Type locality.—Tortugas, [Fla.].

Known range.—Off Cape Lookout, N.C., through eastern Gulf of Mexico, and Yucatan Channel, to Honduras; through West Indies to Venezuela.

Remarks.—This species is not common north of Florida. Ovigerous females are known from March to August in Florida (Rathbun, 1930a, in part) and they have been taken in February in North Carolina.

Pilumnus lacteus Stimpson. Small hairy crab

Figures 157E, 161

Pilumnus lacteus Stimpson, 1871a, p. 142. Hay and Shore, 1918, p. 440, pl. 35, fig. 3.—Rathbun, 1930a, p. 511, pl. 205, figs. 1–2 (rev.).

Recognition characters.—Carapace about three-fourths as long as wide, covered with short velvet-like pubescence easily rubbed off (and often is), nearly smooth, sparse tubercles almost invisible through hairy coating; a row of five tubercles paralleling anterolateral and orbital margins, others scattered. Anterolateral margins with four anteriorly directed teeth, first or outer orbital small. Front depressed, deeply notched in middle, and with a smaller notch near eye. Orbital margin occasionally a bit uneven but not tuberculate.

Chelipeds dissimilar in size but otherwise nearly alike, stout, setose, and plumose-hairy, somewhat tuberculate above, but naked and polished below and on ventral half or two-thirds of both inner and outer surfaces of chelae; merus with two similar curved spines on upper margin distally; carpus with a stout spine on inner angle.

Measurements.—Carapace: male, length, 12 mm.; width, 15 mm.

Color.—Gray or pinkish, with plumose hairs whitish or cream colored; hands and tips of legs light red.

Habitat.—This crab may be found by a careful search of wharf pilings about the Beaufort, N.C., harbor area, but is rarely taken in dredge hauls. It has been taken from buoys both in sounds and at sea in South Carolina (Lunz, 1937a). Rathbun (1930a) reported it from a variety of situations farther south. Near low-tide mark to about 8 fathoms.

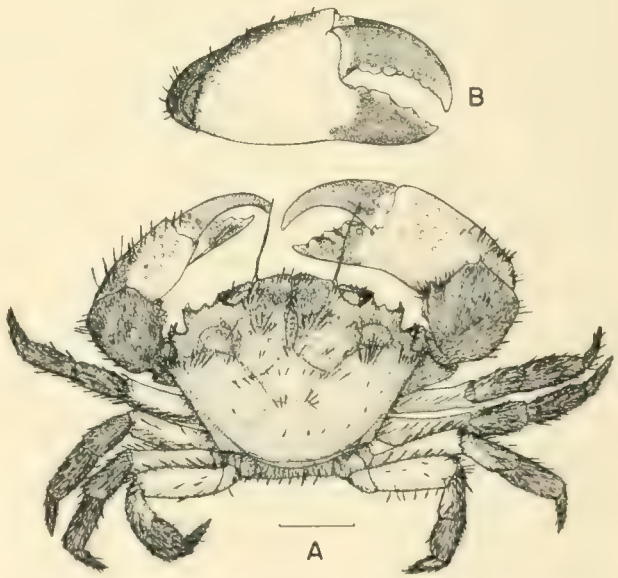

FIGURE 161.—*Pilumnus lacteus* Stimpson. A, animal in dorsal view; B, large chela in frontal view; 5 mm. indicated.

Type locality.—Cruz del Padre, Cuba, and Key West, Fla.

Known range.—Near Beaufort, N.C., to Florida; Cuba.

Remarks.—Ovigerous females have been reported in December from Florida, and in May from Cuba (Rathbun, 1930a) and South Carolina (Lunz, 1937a).

Pilumnus pannosus Rathbun

Figures 157F, 162

Pilumnus pannosus Rathbun, 1896b, p. 142.—Rathbun, 1930a, p. 514, figs. 4–5 (rev.).

Recognition characters.—Carapace about three-fourths as long as wide, almost entirely covered with unevenly distributed, soft, thick, velvety pubescence, with scattered longer club-shaped setae giving ragged appearance; lobulations of anterior portion of carapace and tubercles of chelipeds showing through pubescence. Anterior half of carapace and upper surface of chelipeds and legs dotted with beadlike tubercles. Anterolateral margin with four triangular spines (outer orbital small) having slender forward-projecting tips; subhepatic spine between first and second tooth well developed. Frontal lobes (when well formed) broadly subtriangular, granulate on margin, separated by a V-shaped notch; outer tooth of front almost triangular, acute (blunt at tip in some specimens). Upper margin of orbit with three truncate teeth covered by pubescence, lower margin with a row of short, stout, truncate teeth or tubercles.

Chelipeds with upper surface tuberculate but usually with large part of outer surface smooth and naked; small hand with outer surface often rough with rows of spines; dactyls with a few tubercles near articulation. Male with shallow grooves on fingers, female with well-defined grooves on minor fingers and fixed major finger. Walking legs pubescent, fringed with club-shaped setae mixed with long fine hair.

Measurements.—Carapace: male, length, 9 mm.; width, 12 mm.

Color.—Carapace under pubescence and bare part of palms bright red (Milne Edwards *in* Rathbun, 1930a).

Habitat.—Pearse and Williams (1951) listed this species as taken from a submerged rocky reef, and Rathbun (1930a) listed it from similar situations, as well as from sponges and corals. A few feet to 9 fathoms.

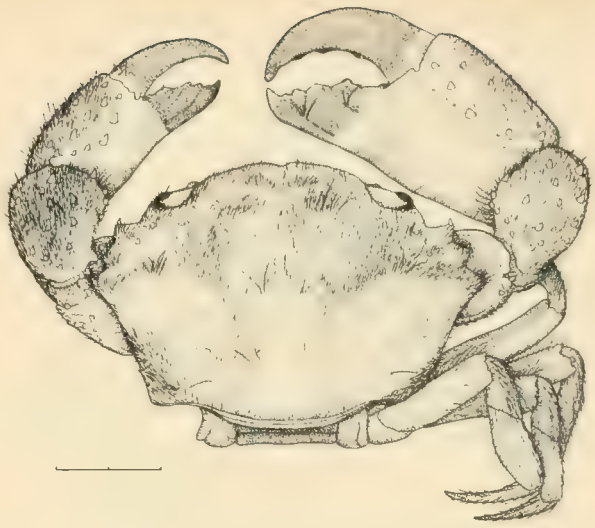

FIGURE 162.—*Pilumnus pannosus* Rathbun. Male in dorsal view, walking legs of left side not shown, 2 mm. indicated.

Type locality.—Key West, Fla.

Known range.—Bogue Sound off Beaufort, N.C., to Port Aransas, Tex.; West Indies to Virgin Islands.

Remarks.—The species has rarely been taken north of Florida. Rathbun (1930a) listed ovigerous females in December and January from Florida, and they are known from April to August between South Carolina and Cuba.

Genus ***Lobopilumnus*** Milne Edwards, 1880

Rathbun, 1930a, p. 525.

Lobopilumnus agassizii (Stimpson)

Figures 157G, 163

Pilumnus agassizii Stimpson, 1871a, p. 142.
Lobopilumnus agassizii: Hay and Shore, 1918, p. 441, pl. 34, fig. 5.—Rathbun, 1930a, p. 526, pl. 211 (rev.).

Recognition characters.—Regions of carapace protuberant, surface pubescent, except naked and thickly granulated on anterior and anterolateral regions; depressions between regions broad, occupying as much area as regions themselves. Front consisting of two large lobate masses deeply separated from each other and from orbits. Orbital region protuberant and granulate, margin crenulated with granules, with two fissures above and two very narrow ones below. Anterolateral margin with three triangular, spine-tipped teeth of moderate, equal size; subhepatic tooth distinct.

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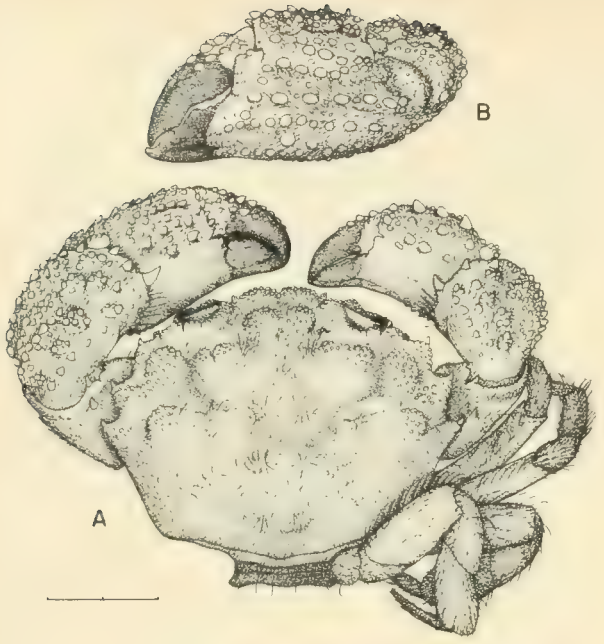

FIGURE 163.—*Lobopilumnus agassizii* (Stimpson). A, male in dorsal view, walking legs of left side not shown; B, large chela in frontal view, 10 mm. indicated.

Chelipeds short, stout; carpus with forwardly directed granules, confluent exteriorly; hands with superior and outer surfaces covered with small prominent mammillary tubercles, arranged largely in rows on outer surfaces and having apices directed forward. Walking legs pubescent and hairy, carpal and propodal articles with minute spines above.

Measurements.—Carapace: female from North Carolina, length, 16 mm.; width, 21 mm.

Variations.—Rathbun (1930a) stated that this species is variable as to the number and prominence of regions on the carapace, and she recognized four environmental forms within the species. Because only one specimen has ever been reported from North Carolina, and this is no longer extant, it is not possible to assign a form or forms to this area.

Color.—Gray above with granules and knobs yellowish red and reddish brown; legs white or with whitish spots (Schmitt *in* Rathbun, 1930a).

Habitat.—In Bermuda, Verrill (1908) found the carapace and legs of this species often thickly covered, sometimes almost concealed, by a coating of calcareous mud and sand adhering to hairs on the back. He found it most frequently under stones and dead corals at low tide. Pearse (1934) reported this crab from loggerhead sponge *Speciospongia vespara* (Lamarck). Low-tide mark to 28 fathoms.

Type locality.—Typical form: East and Middle Keys, Tortugas, Fla.

Known range.—North Carolina; southern and west Florida; Yucatan; Cuba; Trinidad; Bermuda.

Remarks.—Ovigerous females are known from February to July in Florida and Cuba (Rathbun, 1930a, in part).

Genus ***Eriphia*** Latreille, 1817

Rathbun, 1930a, p. 545.

Eriphia gonagra (Fabricius)

Figures 164 A, B, C; 165

Cancer gonagra Fabricius, 1781, p. 505.
Eriphia gonagra: Hay and Shore, 1918, p. 439, pl. 35, fig. 6.-Rathbun, 1930a, p. 545, text-fig. 83, pl. 222 (rev.).

Recognition characters.—Carapace approximately quadrate, about one-fourth wider than long, flattened, with regions clearly marked off on anterior two-thirds; surface nearly smooth posteriorly but granulate anteriorly, and with two transverse lines of subspinous granules, one in front of epigastric lobes and another across protogastric and hepatic lobes. Front wide, strongly deflexed, and divided into four lobes, both median lobes broader and more advanced than lateral ones, and with a finely granulate border. Lateral lobes forming front of raised margin of orbits and in contact beneath with a prolongation of infraorbital plate, thus completely excluding antenna from orbit. Anterolateral margins each with a row of five spines including outer orbital, behind and inside these a few squamiform tubercles.

Chelipeds unequal, strong, swollen; hands covered with large, round, flattened, squamiform tubercles, more elevated on small than on large hand; carpus with less prominent tubercles; dactyls with squamiform tubercles above at base; major dactyl with large rounded tooth at base. Walking legs rather slender, their distal three articles with fine stiff hairs.

Measurements.—Carapace: male, length, 31 mm.; width, 44 mm.

Color.—Gaily colored. Anterior half of carapace and a broad median stripe extending to posterior margin, dark purplish brown, legs a lighter tint of same color; front margined with brownish orange. Sides of carapace, upper surface of chelipeds, dactyls, bases of legs, and a narrow band on distal margin of other articles, light yellow. Tubercles on upper half of chelipeds, dark blue; on lower half, yellow. Underparts of body and chelipeds, white, fingers brown. Rathbun (1930a) gives another detailed color description.

Habitat.—The species has been found in a variety of situations: under flat rocks above the watermark, in seaweed, sponges, brackish ponds, tide pools, and on coral reefs. Shoreline to shallow water of uncertain limits.

FIGURE 165.—*Eriphia gonagra* (Fabricius). Male in dorsal view, walking legs of left side not shown, 10 mm. indicated.

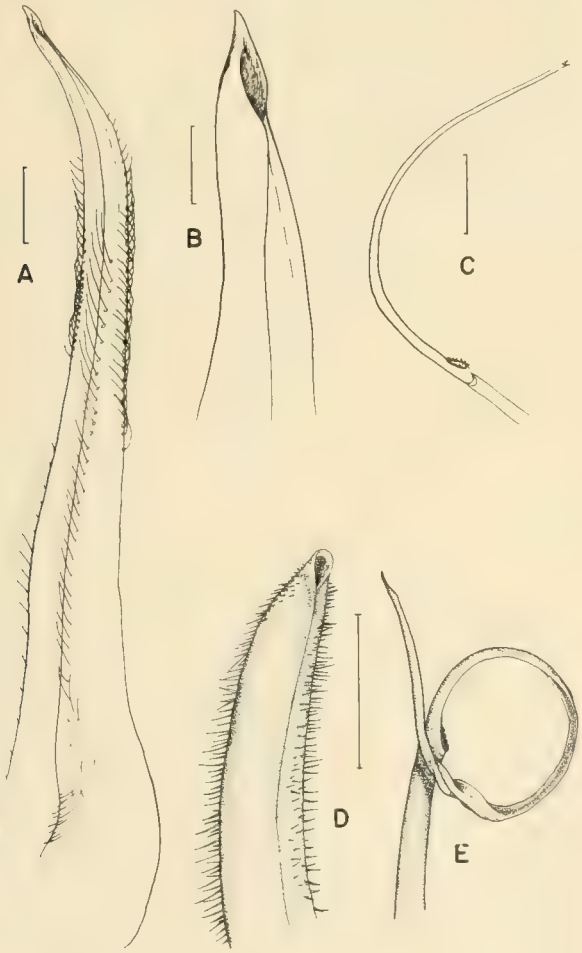

FIGURE 164.—*Eriphia gonagra* (Fabricius); A, entire first pleopod, 0.75 mm. indicated; B, tip of first pleopod, 0.25 mm. indicated; C, tip of second pleopod, 0.75 mm. indicated; *Menippe mercenaria* (Say); D, tip of first pleopod; E, tip of second pleopod; 5 mm. indicated.

Type locality.—Jamaica.

Known range.—North Carolina to Argentine Patagonia.

Remarks.—Ovigerous females are known from March to September in various parts of the West Indies and southern Florida; in October from Santa Catarina, and February from Bahia, Brazil (Rathbun, 1930a, in part).

Genus ***Menippe*** de Haan, 1833

Rathbun, 1930a, p. 472.

Menippe mercenaria (Say). Stone crab

Figures 164 D, E; 166

Cancer mercenaria Say, 1818, p. 448.

Menippe mercenaria: Hay and Shore, 1918, p. 439, pl. 35, fig. 8.—Rathbun, 1930a, p. 472, text-fig. 78, pls. 191–193 (rev.).

Recognition characters.—Carapace transversely oval, approximately two-thirds as long as wide, convex, nearly smooth to unaided eye, minutely granulate and punctate. Anterolateral border divided into four lobes: first two wide, third wide but dentiform, fourth much narrower and dentiform. Front with a median notch and a broad trilobulate lobe on each side. Orbital border thick, fissures indistinct.

Chelipeds large and heavy, unequal, nearly smooth; inside surface of hands with a patch of fine, oblique, parallel striae serving as a stridulating organ and adapted for playing against thick edge of second and third anterolateral teeth and

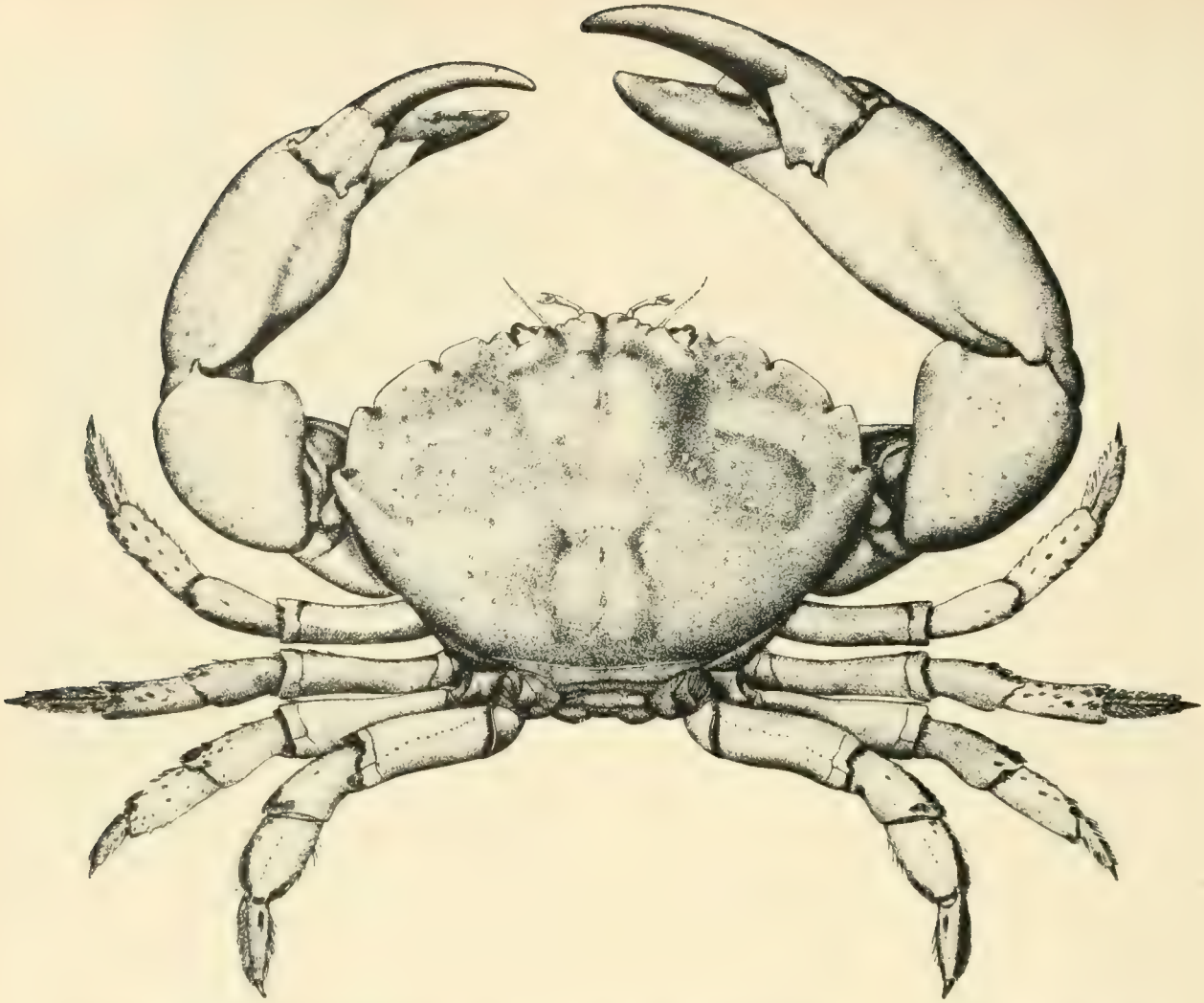

FIGURE 166.—*Menippe mercenaria* (Say). Male in dorsal view, approximately × 0.6 (after Rathbun, 1884).

outer suborbital tooth; dactyl of major chela with a large basal tooth, and immovable finger with a large subbasal tooth; fingers of minor chela with numerous small teeth. Walking legs stout, hairy distally.

Measurements. Female: length of carapace, 79 mm., width, 116 mm.; length of cheliped, 155 mm. This is the largest xanthid species in the area.

Color.—Young individuals dark purplish blue, very young always with a white spot on carpus. Older individuals become a dark brownish red more or less mottled and spotted with dusky gray; fingers dark.

Habitat. The young resort to deeper channels of saltier estuaries where they live under shell fragments. Young have also been taken from buoys in South Carolina (Lunz, 1937a). On attaining a width of about one-half inch, they apparently move to shallower water and may be found among oyster shells, on rocks, pilings, and about jetties. (In northwest Florida, *M. mercenaria* apparently prefers turtle grass (*Thalassia testudinum*) flats (Wass, 1955).) Here they live until they have attained nearly full size when they may move to some shoal and make burrows just below low-tide mark. Such burrows are about 6 inches in diameter and extend for 12 to 20 inches. The crabs can be taken from burrows by hand if the collector keeps his hand against the upper wall of the hole, and a number of specimens for

the Institute of Fisheries Research Laboratory have been taken in this manner. Specimens have also been taken from baited plots set for capture of blue crabs, and in trawls from the oceanic littoral. Surface to 28 fathoms.

Type locality.—"The Southern States."

Known range.—Cape Lookout, N.C., to Yucatan, Mexico; Bahamas; Cuba; Jamaica.

Remarks.—The genus *Menippe* has a fossil record in North America dating from the Cretaceous, the thick, hard exoskeleton no doubt enhancing its chances of fossilization. The record for *M. mercenaria* dates from the Pleistocene (Rathbun, 1935).

Ovigerous females have been taken from May to July (perhaps August) in North Carolina. Binford (1912) discussed spermatogenesis and fertilization in the species and gave notes on spawning habits. Porter (1960) reviewed literature on fecundity and larval development of *M. mercenaria* and described zoeal stages reared in the laboratory. Females have been observed to molt, then mate immediately after spawning in the laboratory, and produce a new sponge a week after the previous egg mass has hatched. Subsequent to such mating, more than one mass of eggs may be produced before another molt or mating occurs. Females have been known to produce six egg masses in 69 days, each mass containing between 500,000 and 1 million viable eggs.

Porter described one prezoeal and six zoeal stages for larvae reared in culture on *Artemia* nauplii, but the prezoeal and sixth stages were considered as probably atypical. Length of larval life was approximately 27 days under the conditions imposed, and from experimental data it was concluded that warm water of high salinity is needed for optimum survival.

Manning (1961) gave data on relative growth, showing that the juveniles have a relatively broader front than adults. Both he and Wass (1955) pointed out the superficial resemblance of young *M. mercenaria* to *Panopeus herbstii* and *Eurytium limosum*, and Manning gave distinguishing characters for each species at comparable sizes. Further, the stridulating mechanism was shown not to be visible in small specimens and, indeed, stridulation itself has not been observed in the adults (Guinot-Dumortier and Dumortier, 1960).

In studies on the relationship of number and volume of gills to oxygen consumption, Pearse (1929) and Ayers (1938) found this form, along with other mud crabs, intermediate between the sluggish common spider crab and the more active, partially terrestrial, fiddler and ghost crabs. Pearse also found that *M. mercenaria* could withstand considerable dilution of the environment with fresh water. Gray (1957) found gill area per gram of weight to be intermediate in an array of species ranging from land to shallow-water habitats.

Menzel and Hopkins (1956) found the stone crab in Louisiana to be an active predator on oysters. The powerful crabs killed small and large oysters alike. Though predation was found to be lowest in winter and highest in fall, the average rate of consumption in the area studied was 219 oysters per crab per year (=1,000 bushels of oysters per acre if this number were available).

Genus ***Glyptoxanthus*** Milne Edwards, 1879

Rathbun, 1930a, p. 263.

Glyptoxanthus erosus (Stimpson)

Figures 167, 183A

Actaea erosa Stimpson, 1859, p. 51.
Glyptoxanthus erosus: Rathbun, 1930a, p. 263, pl. 107 (rev.).

FIGURE 167.—*Glyptoxanthus erosus* (Stimpson). Animal in dorsal view, detail shown on right side, 5 mm. indicated.

Recognition characters.—Surface of body and legs covered with rough vermiculations, with furrows or cavities between them narrow, making a regular pattern and giving body an eroded appearance; elevated portions between furrows or cavities formed by masses of small granules crowded together producing rough surface in young and half-grown individuals, but variably worn smooth in old ones; margins of cavities with short pubescence. Carapace areolated, but divisions obscured to large extent by character of surface; lateral boundaries of gastric region and median suture from front to middle of gastric region deep. Front steeply inclined, median lobes evenly rounded, margins granulate. Ischium of third maxilliped with deep, longitudinal, central groove.

Chelae short and broad, upper surface divided by furrows into transverse tuberculate ridges, outer surface divided into longitudinal tuberculate ridges; fingers short, deeply grooved, even toothed; dactyls tuberculate at base on upper side. Walking legs with hairy edges, dactyls pubescent.

Measurements.—Carapace: male, length, 39 mm.; width, 54 mm.

Color.—Rathbun (1930a) described a specimen in formalin as cream white with blotches and small spots of bright red, color especially persistent on walking legs, with dactyls red at base and yellowish distally.

Habitat.—The species has been taken from rocks and the alga *Halimeda* in shallow water, from coarse sand, and from sponges and coral reefs in deeper water. Low-tide mark to 37 fathoms.

Type locality.—Florida.

Known range.—Cape Lookout, N.C., to Yucatan; through West Indies to Guadeloupe.

Remarks.—Ovigerous females have been taken off northeast Florida in January.

Genus ***Carpoporus*** Stimpson, 1871

Rathbun, 1930a, p. 269.—Hemming, 1958b, p. 14.

Carpoporus papulosus Stimpson

Figure 168, 183B

Carpoporus papulosus Stimpson, 1871a, p. 139. Rathbun, 1930a, p. 269, pl. 110, figs. 3–6, pl. 111 (rev.).

Recognition characters.—Carapace subhexagonal, nearly as long as broad, naked above; regions

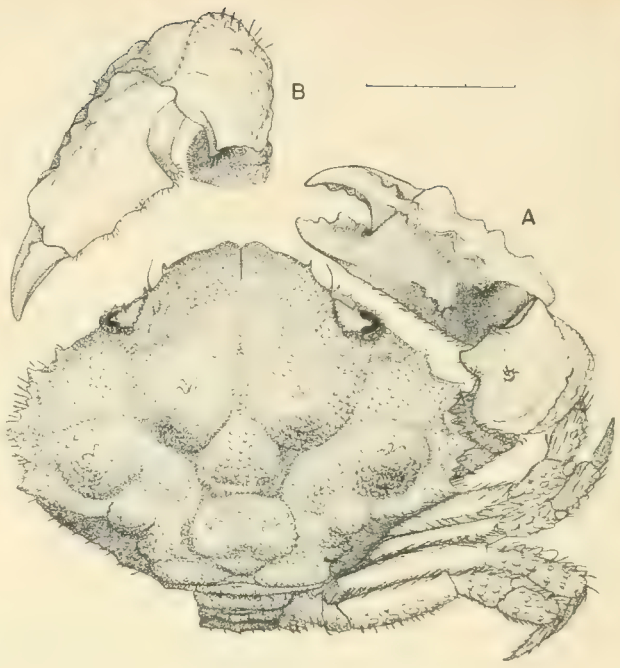

FIGURE 168.—*Carpoporus papulosus* Stimpson. A, animal in dorsal view, legs of left side not shown; B, cheliped in frontal view partially extended; 3 mm. indicated.

protuberant, somewhat wartlike and granulated, gastric and epibranchial regions prominent. Two or three small, spiniform lateral teeth, interspaces armed with denticles. Front strongly projecting at middle, bilobed, margin concave, inner end rectangular, outer end spiniform. Peduncle of eye granulated; orbit with margin granulate above. Exposed surface of third maxilliped with beadlike granules.

Chelipeds when retracted having a large hole between carpus and hand for passage of water to afferent branchial apertures; inner surface of hand with two unequal peglike spines near middle forming a kind of filter in front of branchial opening; carpus and hand sculptured externally with granulated protuberances, arranged in four or five serial rows on hand; hand serrate above with four teeth partially joined; fingers stout, short. Walking legs hairy below.

Measurements.—Carapace: male, length, 13 mm.; width, 16 mm.

Habitat.—Eighteen to 62 fathoms.

Type localities.—Southwest of Tortugas, and off Carysfort Reef, [Fla.].

Known range.—Between Capes Hatteras and Lookout, N.C.; Cape Catoche, Yucatan, Mexico.

Genus *Rhithropanopeus* Rathbun, 1898

Rathbun, 1930a, p. 455.—Hemming, 1958b, p. 37.

Rhithropanopeus harrisii (Gould)

Figures 169, 183C

Pilumnus harrisii Gould, 1841, p. 326.
Rhithropanopeus harrisii: Hay and Shore, 1918, p. 441, pl. 35, fig. 5.—Rathbun, 1930a, p. 456, pl. 183, figs. 7–8 (rev.).

Recognition characters.—Carapace subquadrate, approximately three-fourths as long as wide, much less convex from side to side than from front to back, sparsely pubescent toward anterolateral angles; protogastric regions with two transverse lines of granules; a similar line from one posterior lateral tooth to opposite one across mesogastric region. Front almost straight, slightly notched, and with margin transversely grooved, appearing double when viewed from in front. Postorbital angle and first anterolateral tooth completely coalesced; first and second developed anterolateral teeth of about same size and perhaps larger than last one.

Chelipeds unequal and dissimilar; carpus not grooved above and with a moderately developed internal tooth; chelae indistinctly costate above. Major chela with short immovable finger and strongly curved dactyl. Minor chela with proportionately longer immovable finger and long straight dactyl. Walking legs long, slender, compressed, and somewhat hairy.

Measurements.—Carapace: male, length, 15 mm.; width, 19 mm.

Variations.—The chelipeds are nearly smooth in old individuals, but in small specimens the carpus is rough with lines and bunches of granules, the distal groove deep, the upper margin of palm with two granulate ridges, and the upper edge of the fingers granulate.

Color.—Brownish above, paler below; fingers light.

Habitat.—In Chesapeake Bay, Ryan (1956) found this species distributed primarily in the upper bay and in tributaries of the lower bay in depths of 0 to 5 fathoms. A similar distribution has been found for upper Delaware Bay (McDermott and Flower, 1953) and the tributaries of the Neuse River estuary in North Carolina. Ryan collected specimens in waters ranging from fresh to 18.6‰. The places from which the form was taken always afforded some kind of shelter—oyster bars, living and decaying vegetation, old cans, and other debris. Bousfield (1955) found larvae of the species in water from 4 to no higher than 28.5 ‰ salinity. Surface to 20 fathoms.

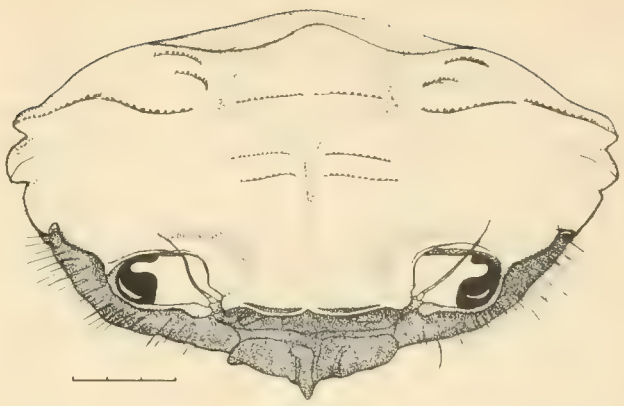

FIGURE 169.—*Rhithropanopeus harrisii* (Gould). Frontal aspect of body viewed from above, 3 mm. indicated.

Type locality.—Cambridge Marshes and Charles River, Mass.

Known range.—The original range of this species was in fresh to estuarine waters from New Brunswick, Canada, to Veracruz, Mexico; northeast Brazil. The species has been introduced on the west coast of the United States and in parts of Europe.

Remarks.—Connolly (1925) stated that four zoeal stages and one megalops stage comprise the larval and postlarval development of this species. These conclusions were based on study of plankton taken from the Miramichi River estuary, New Brunswick, Canada, in August. Chamberlain (1962) confirmed and supplemented Connolly's account with eggs taken from Chesapeake Bay and cultured in the laboratory. Duration of larval stages was twice as long when zoeae were fed copepod nauplii and algae as when fed nauplii alone. In an array of salinities and temperatures, development was found to proceed best at 6 to 10 ‰ salinity. Developmental time increased with decreasing temperature. Developmental times of larvae in nature were found to be in agreement with results of laboratory culturing at similar salinities and temperatures. Mortality rates for larvae in nature were found to be lower than expected. A relatively high rate was postulated for the megalops or early crab stages. Presence of adult crabs in fresh water was deemed a result of migration after larval stages are complete. Hood

(1962) also described a series of larval and post-larval stages from eggs hatched and reared under laboratory conditions in Mississippi.

Ryan (1956) summarized life history data for *R. harrisii* in the Chesapeake Bay area. Ovigerous females were collected from June to September (also in April in Louisiana and Brazil). Though juveniles were found in all months of the year, they occurred most frequently in samples taken from July to October. Immature forms of undetermined sex ranged from 2.2 to 2.6 mm. in width. Immature males ranged from 3.2 to 5.0 mm. and similar females from 3.3 to 5.7 mm. in width. Ryan considered maturity to be reached the following summer at a carapace width of 4.5 mm. for males and 4.4 to 5.5 mm. in females.

Adults continue to grow and molt after maturity is reached, and males finally attain a larger size than females (up to 14.6 and 12.6 mm. wide respectively). No concrete data on number of instars throughout life are available but it is estimated that there may be four instars between attainment of the 5 and 10 mm. carapace widths.

This species has been transported from its original range to two widely separated areas of the earth. One of these is the west coast of the United States where it was reported in the San Francisco Bay area by Jones (1940) and Filice (1958), and at Coos Bay, Oreg., by Ricketts and Calvin (1952). An older and wider introduction in Europe was reviewed by Buitendijk and Holthuis (1949) who considered the European form a separate subspecies (*R. h. tridentatus* (Maitland)). Originally confined to the old Dutch Zuider Zee, the species gradually diminished in abundance there with the closing of that inland sea in 1936. In that same year it was first reported outside Netherlands waters. In 1939 it was first reported in large numbers from southern Russia in the Dnjetr and Bug River estuaries, and according to fisherman there was first observed in 1936 but certainly not present before 1932. The latest extension of range was reported by Wolff (1954) in South Harbor of Copenhagen, Denmark.

Because this form is easily collected and can tolerate a low but broad range of salinities, it has been the subject of study in investigations on the mechanism of osmoregulation (Jones, 1941; Verwey, 1957).

Genus *Hexapanopeus* Rathbun, 1898

Rathbun, 1930a, p. 383.

KEY TO SPECIES IN THE CAROLINAS

a. Carpus slightly tuberculate_____*angustifrons* (p. 188).
aa. Carpus tuberculate_____*paulensis* (p. 189).

Hexapanopeus angustifrons (Benedict and Rathbun). Narrow mud crab

Figures 170, 183D

Panopeus angustifrons Benedict and Rathbun, 1891, p. 373, pl. 22, fig. 3; pl. 24, fig. 18.
Hexapanopeus angustifrons: Hay and Shore, 1918, p. 436, pl. 34, fig. 7.—Rathbun, 1930a, p. 384, pl. 169, figs. 1–2 (rev.).

Recognition characters.—Carapace hexagonal, about two-thirds to three-fourths as long as wide, convex from front to back, regions fairly well marked, surface finely granulate. Anterolateral edge thin, upturned, and divided into five teeth, first two separated by a well-defined sinus, third and fourth successively broader, fifth shorter, narrower, more distinctly directed outward; each of last two teeth with a ridge extending obliquely inward and backward for distance twice length of teeth. Front narrow, produced, divided in half by a prominent V-shaped notch; each half bilobate, with markedly sinuate anterior border forming a broad inner and small, inconspicuous outer lobe.

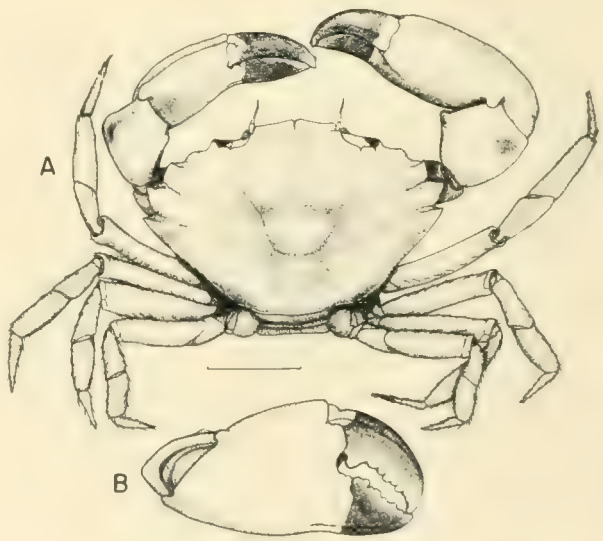

FIGURE 170.—*Hexapanopeus angustifrons* (Benedict and Rathbun). A, animal in dorsal view; B, large chela in frontal view; 5 mm. indicated.

Chelipeds strong, granulate, and finely rugose; merus with a well-developed tooth on upper margin; carpus with a moderately deep groove parallel to distal margin, an obtuse tooth at inner angle, and with superior surface rough and more or less tuberculate. Hands unequal and dissimilar; palm usually with a fairly strong ridge above and indications of one on outer surface, both ridges continued on fingers; fingers strong, slightly hooked at tips; dactyl of larger hand with strong tooth at base.

Measurements.—Carapace: length, 20 mm.; width, 28 mm.

Color.—Usually dark reddish brown or dark gray, sometimes a uniform brownish yellow or light buff; females usually darker than males and often more or less spotted; fingers black or dark brown at base, lighter at tips, color not continued on palm. Often a light yellow band along anterior border of carapace (Wass, 1955, in part).

Habitat.—Ryan (1956) found this species infrequently in the lower portion of Chespeake Bay in from 6- to 25-fathom water (Cowles, 1930, in part) and in salinities ranging from 18 to 32‰. McDermott and Flower (1953) found the species only in the lower portion of Delaware Bay. Rathbun (1930a) recorded the species from oyster bars along the New England coast, and it is found in shelly situations in the Carolinas (Lunz, 1937a). Though it occurs in places such as Beaufort Harbor, N.C., the species is apparently not found primarily in shallow water near shore (see also Wass, 1955). Near shore to 76 fathoms.

Type locality.—Long Island Sound.

Known range.—Vineyard Sound, Mass., to Port Aransas, Tex.; Bahamas; Jamaica.

Remarks.—Ovigerous females are known from February to August in Florida, in July from North Carolina and Virginia, and in October from Texas. Ryan (1956) gave the range in carapace width of mature males as 9.7 to 28.9 mm. and of mature females as 8.4 to 20.2 mm. in Chesapeake Bay. Rathbun (1930a) considered specimens from Chesapeake Bay southward to average smaller than those from farther north.

Chamberlain (1961) reported four zoeal stages and one megalops stage in larval development of the species but did not describe the stages in detail. He found that larval development time varied with temperature (17 days at 30° C., 28 at 21° C.) and with food. Larvae matured most rapidly when fed *Artemia salina* nauplii, matured moderately well on *Artemia* and algae, but did not transform at all when fed algae alone.

Hexapanopeus paulensis Rathbun

Figures 171, 183E

Hexapanopeus paulensis Rathbun, 1930a, p. 395, pl. 170, figs. 5–6.

Recognition characters.—Carapace hexagonal, approximately two-thirds to three-fourths as long as wide, convex, regions fairly well marked, surface with approximately 12 transverse granulated lines on gastric, cardiac, and branchial regions. First tooth of anterolateral border small; second larger, broad, and shallow, with arcuate outer margin; third with nearly straight margin directed forward and inward; fourth and fifth acute and prominent; sometimes with small denticle between first, second, or third pairs of teeth. Front with edge thin, arcuate, with small, median, V-shaped notch, and each half with small lobule at outer end. Inner suborbital angle large; a raised line of granules on subhepatic region.

Chelipeds with carpus and upper part of palm roughened; carpus with approximately 15 tubercles above, an internal tooth, and below it a small tooth or denticle, distal groove deep. Hand with a superior groove and another on outer surface below upper edge, ridges bordering groove with low tubercles; fingers deeply grooved, dark or horn colored, color continued somewhat on palm, ending in an oblique line; tips light.

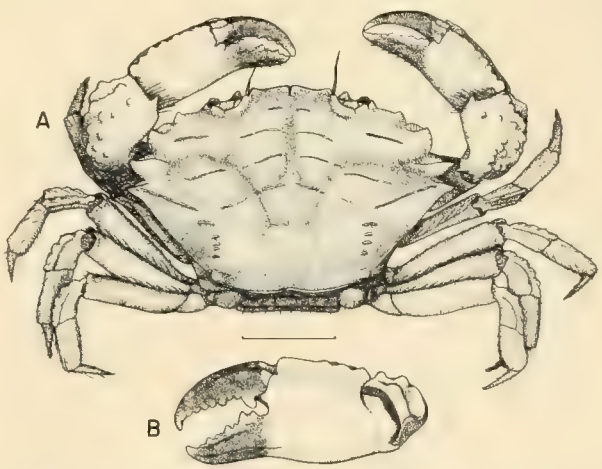

FIGURE 171.—*Hexapanopeus paulensis* Rathbun. A, animal in dorsal view; B, large chela in frontal view; 5 mm. indicated.

Measurements.—Carapace: male, length, 7 mm., width, 10 mm.; female, length, 10 mm., width, 14 mm.

Habitat.—Three fathoms (Lunz, 1937a).

Type locality.—Santos, São Paulo, Brazil.

Known range.—South Carolina, through Gulf of Mexico to State of São Paulo, Brazil.

Remarks.—This species has been reported from only a few widely separated areas. Rathbun (1930a) reported ovigerous females in September from Brazil.

Genus *Neopanope* Milne Edwards, 1880

Rathbun, 1930a, p. 366.

KEY TO SUBSPECIES IN THE CAROLINAS

a. Fingers white or light horn colored
texana texana (p. 190).

aa. Fingers dark colored—*texana sayi* (p. 190).

Neopanope texana texana (Stimpson)

Figures 172, 183F

Panopeus texanus Stimpson, 1859, p. 55.

Neopanope texana texana: Rathbun, 1930a, p. 367, text-fig. 57, pl. 168, figs. 1–2 (rev.).

Recognition characters.—Carapace quite convex in both directions, high in middle, length contained in width about 1.3 times, greatest width at fifth pair of anterolateral teeth. Carapace minutely pubescent, especially in female; regions defined. First two anterolateral teeth coalesced, separated by a shallow sinus; first tooth triangular, second arcuate; third and fourth teeth sharp, with tips pointing forward; fifth tooth short, sharp, directed outward and upward; each of last two teeth with a short ridge extending inward. Front slightly produced, rounded, with small median notch.

Chelipeds smooth, unequal, and dissimilar; carpus with subdistal groove, fingers white or horn colored in males, somewhat darker in females, color extending somewhat on palm and terminating in a distinct line; no large tooth at base of major dactyl. Walking legs long and slender.

Measurements.—Carapace: male, length, 21 mm.; width, 27 mm.

Variations.—In individuals 14 mm. wide and smaller, the carpus is much rougher than that described above, has a sharper internal spine, and a longitudinal groove on the upper surface of the palm. In individuals with a carapace width less than 5 mm., the first and second anterolateral teeth are completely coalesced. Where the ranges of *N. t. texana* and *N. t. sayi* overlap, specimens are often found which share characters of both subspecies (Rathbun, 1930a, p. 370, in part).

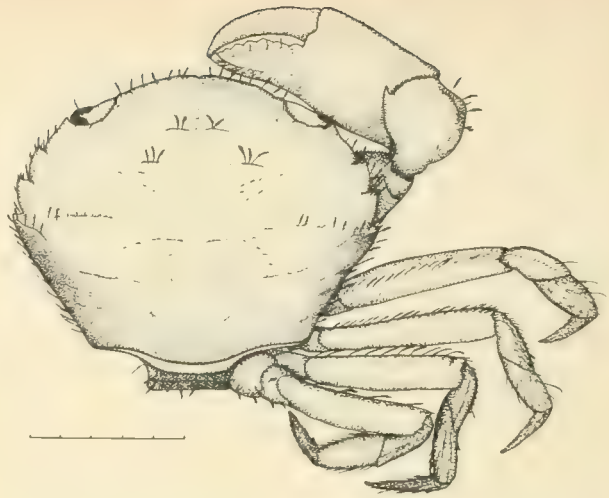

FIGURE 172.—*Neopanope texana texana* (Stimpson). Male in dorsal view, legs of left side not shown, 5 mm. indicated.

Color.—Body mottled gray; a roughly W-shaped grayish configuration on anterior half of carapace with its anterior points located in midline and behind orbits, and a less definite continuation of this figure extending toward anterolateral borders; hands of chelipeds mottled gray, fingers with light tips; walking legs with narrow gray cross bands alternating with lighter ground color.

Habitat.—Most abundant in shallow water where bottom is soft and there is vegetation (Wass, 1955). Low tide to 28 fathoms.

Type locality.—St. Josephs Island, Tex.

Known range.—York River, Va., via Florida Keys and Gulf coast to Laguna Madre, Tamaulipas, Mexico.

Remarks.—Ovigerous females have been reported in March from Florida (Rathbun, 1930a), and they are known from North Carolina in July and August.

Neopanope texana sayi (Smith)

Figures 173, 183G

Panopeus sayi Smith, 1869a, p. 284.

Neopanope texana sayi: Hay and Shore, 1918, p. 438, pl. 34, fig. 8.—Rathbun, 1930a, p. 369, text-fig. 58, pl. 168, figs. 3–4 (rev.).

Neopanope texana nigrodigita Rathbun, 1934, pp. 3–4, illus.

Recognition characters.—Carapace subhexagonal, length contained in width about 1.3 to 1.4 times, greatest width at fifth pair of anterolateral teeth, quite convex; carapace minutely granulate, and lightly pubescent especially near anterior and lateral regions. Five anterolateral teeth, first two coalesced and separated by a shallow sinus, third and fourth larger and directed forward, fifth smaller and directed somewhat outward; each of last two teeth with an oblique ridge extending inward and backward. Front with small median notch, each half only slightly sinuate, with whole forming a much flattened curve extending from eye to eye.

Chelae barely unequal, smooth, dissimilar; carpus and merus with a shallow groove parallel to distal margin, and usually a blunt internal spine; major dactyl without large basal tooth, fingers of minor chelae not spoon shaped.

Resembles *Eurypanopeus depressus.*

Measurements.—Carapace: length, 17 mm.; width, 23 mm.

Variations.—Where the ranges of *N. t. texana* and *N. t. sayi* overlap, specimens are often found which share characters of both subspecies (Rathbun, 1930a, p. 370, in part).

Color.—Carapace a dark, slaty bluish green, brown or buff, with dark reddish-brown speckles on yellowish background, or bluish purple on gray background, especially on anterior portion of carapace and upper portion of chelae; outer face of chelae yellowish gray; fingers dark or black, color extending extensively on palm, tips light.

Habitat.—Most studies indicate greatest abundance on mud bottoms, though the form occurs in other situations as well, and in the Chesapeake area in a salinity range of 14.66 to 31.62 °/₀₀ in a dry year. Low-tide mark to 15 fathoms.

Type localities.—New Haven, Conn., and Cape Cod, Mass.

Known range.—Miramichi Bay, Prince Edward Island and Cape Breton Island, New Brunswick, Canada (Bousfield, 1956), to eastern Florida. Introduced, Swansea, Wales (Naylor, 1960).

Remarks.—Rathbun's subspecies *N. t. nigrodigita* is here regarded as conspecific with *N. t. texana* on the basis of examination of a series of specimens in the Charleston Museum. Rathbun (1930a) reported the largest male on record as 27.2 mm. wide.

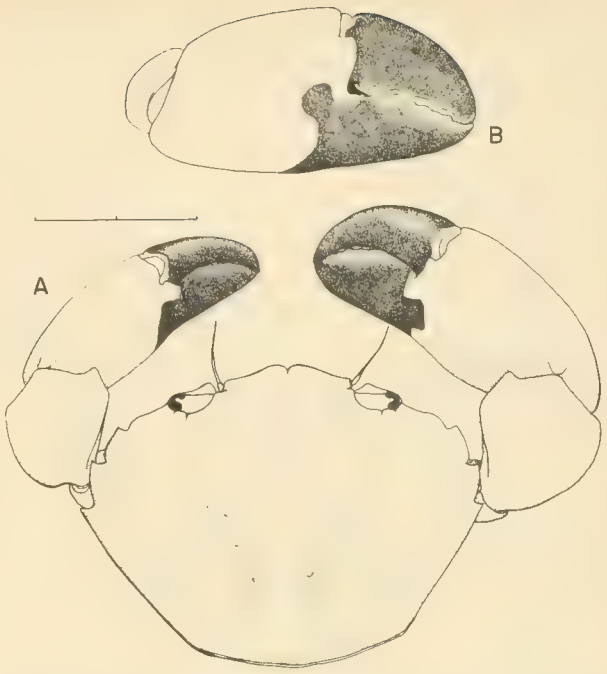

FIGURE 173.—*Neopanope texana sayi* (Smith). A, male in dorsal view, walking legs not shown; B, large chela in frontal view; 10 mm. indicated.

Ovigerous females have been taken from April in South Carolina (Lunz, 1937a) to October in Chesapeake Bay. Cowles (1930) found young individuals during fall, winter, and spring in Chesapeake Bay, and concluded that juveniles reach maturity the first summer after hatching. Ryan (1956) summarized the work of Hyman (1925) on zoeal and megalops stages, and gave some data on size at maturity. He concluded that mature females ranged in width from 6.1 to 18.7 mm.

Chamberlain (1957, 1961) discussed development time and stages in detail. He found development limited to four zoeal stages (sometimes preceded by a brief prezoeal stage) and one megalops stage. Developmental time varied with temperature (14 days at 30° C., 27 at 21° C.) and with food. Larvae matured most rapidly when fed *Artemia salina* nauplii, did moderately well on *Artemia* and algae, but did not transform at all when fed pure algae.

McDermott and Flower (1953) considered this form to be the most abundant mud crab in Delaware Bay, but within the area studied it was more common on oyster beds than in littoral or low-

salinity areas. They found (also McDermott, 1960) that *N. t. sayi* readily preys on *Balanus improvisus*. Farther north, Landers (1954) reported the crab abundant in Narragansett Bay where it is a serious predator on young *Mercenaria mercenaria*. Ryan (1956) found the form widely distributed in Chesapeake Bay, but apparently not so abundant as in the more northern bays. Here it ranged in depth from 2 to 25 fathoms (Rathbun, 1930a, in part), depths similar to those reported by Sumner, Osburn, and Cole (1913a, b) for the Woods Hole region.

Genus ***Leptodius*** Milne Edwards, 1863

Rathbun, 1930a, p. 296.—Hemming, 1958b, p. 33.

Leptodius agassizii Milne Edwards

Figures 174, 183H

Leptodius agassizii Milne Edwards, 1880, p. 270, pl. 49, fig. 3.—Hay and Shore, 1918, p. 441, pl. 34, fig. 6.—Rathbun, 1930a, p. 307, pl. 141, figs. 4–5 (rev.).

Recognition characters.—Carapace broad, suboval, flattened, and finely granulate posteriorly, conspicuously sculptured anteriorly; regions lobulate, with coarse granules and fine scattered hairs along front margin of lobules. Frontal margin transversely grooved, appearing double; upper margin less pronounced than lower, with groove extending across from orbit to orbit, both edges of groove and orbital margin granulate. Of five anterolateral teeth only last two or three well developed, sharp, and turned forward; second tooth, and sometimes third, triangular and obtuse, first (outer orbital angle) represented by an elevated mass of granules.

Chelipeds unequal; larger one with strong, blunt-tipped fingers; smaller one with more slender, more acute, and more conspicuously grooved fingers showing tendency to be spoon shaped at tips; fingers dark, both hands with upper and outer surfaces granulate and tuberculate and with tubercles arranged in rows; carpus strong, with a sharp internal spine, sometimes a double spine, and with many irregular, granulate rugae above. Walking legs granulate and hairy.

Measurements.—Carapace: male, length, 8 mm., width, 12 mm.; ovigerous female, length, 20 mm., width, 31 mm.

Variations.—Small specimens from near Beaufort, N.C., have the last three anterolateral teeth well developed, but a series in the U.S. National Museum from Pensacola, Fla., shows that the number of these spines may be reduced to two in larger individuals.

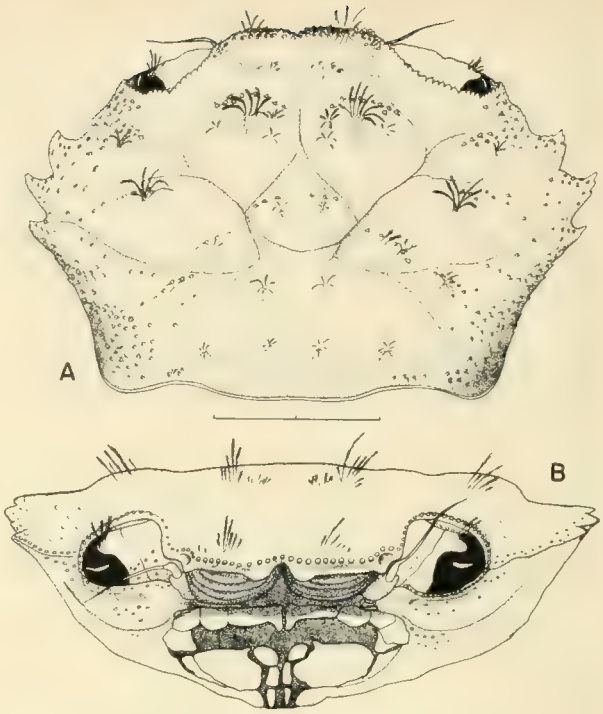

FIGURE 174.—*Leptodius agassizii* Milne Edwards. A. carapace in dorsal view; B, carapace in frontal view; 2 mm. indicated.

Color.—After a short preservation in alcohol, light red, fingers black.

Habitat.—This species has been taken from coral rock, sponges, and on sandy bottom. Approximately 6 to 45 fathoms.

Type locality.—Florida Reefs, 12 to 18 fathoms.

Known range.—Cape Hatteras, N.C., to Pensacola, Fla.; Virgin Islands.

Remarks.—Ovigerous females are known from April to November in various parts of the range.

Genus ***Micropanope*** Stimpson, 1871

Rathbun, 1930a, p. 426.—Hemming, 1958b, p. 34.

KEY TO SPECIES IN THE CAROLINAS

a. Last lateral tooth of carapace obsolescent, carapace rough, legs spinulose ..... *sculptipes* (p. 193).

aa. Last lateral tooth of carapace small but easily discernible.

b. Second lateral tooth present, last lateral tooth deniform, not spinose; outer surface of hand somewhat rugose ..... *xanthiformis* (p. 193).

bb. Second lateral tooth absent or fused with first; outer surface of hand rough with large beadlike granules ..... *nuttingi* (p. 194).

Micropanope sculptipes Stimpson

Figure 175

Micropanope sculptipes Stimpson, 1871a, p. 140.—Rathbun, 1930a, p. 428, pl. 178, figs. 1–3 (rev.).

Recognition characters.—Carapace naked, distinctly areolated; anterior and anterolateral regions somewhat roughened in front with small, sharp, toothlike tubercles partially disposed in lines. Anterolateral teeth sharp, denticulate, fifth (last) obsolescent, first and second almost entirely fused. Frontal lobes abruptly deflexed, with convex outline; margin thin, minutely crenulate, with slight furrow above it. A small tubercle on subhepatic region below second anterolateral tooth.

Chelipeds granulate above; carpus with granules arranged more or less in raised reticulated rugae, inner margin denticulate and with a sharp spine; hand with double denticulate crest above and with minute granules on outer surface showing tendency to arrangement in rows, becoming obsolete in distal lower half of major chela, upper part of inner surface granulate; fingers grooved, with a thin superior crest on dactyls. Walking legs with minute spines above forming two rows on carpus.

Measurements.—Carapace: male, length, 4 mm.; width, 6 mm.

Habitat.—Fifteen to 101 fathoms.

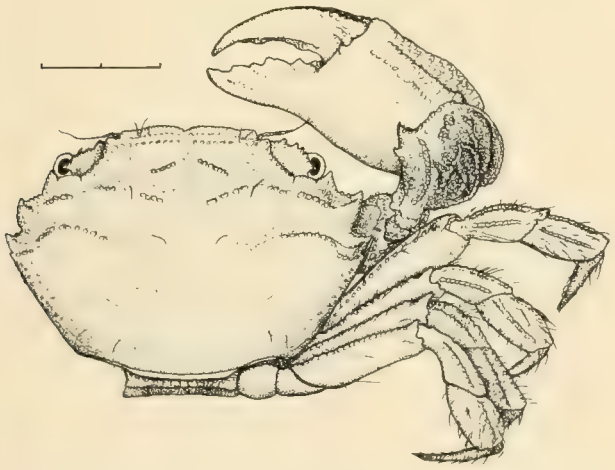

FIGURE 175.—*Micropanope sculptipes* Stimpson. Animal in dorsal view, legs of left side not shown, 2 mm. indicated.

Type locality.—Florida Keys.

Known range.—South Carolina to Port Aransas, Tex.; West Indies to Barbados.

Micropanope xanthiformis (Milne Edwards)

Figures 176, 183I

Panopeus xanthiformis Milne Edwards, 1880, p. 353, pl. 53, figs. 4–4b.—Rathbun, 1930a, p. 442, pl. 180, figs. 7–8 (rev.).

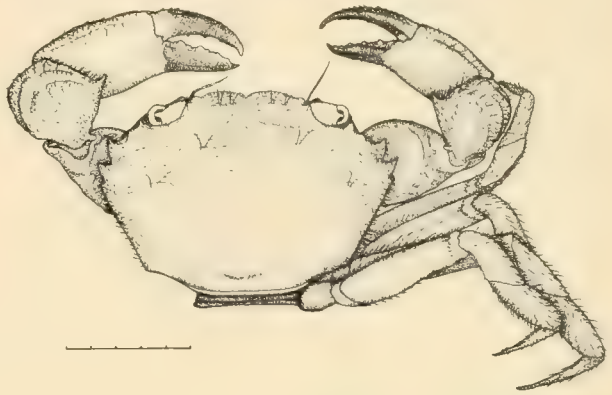

FIGURE 176.—*Micropanope xanthiformis* (Milne Edwards). Animal in dorsal view, walking legs of left side not shown, 5 mm. indicated.

Recognition characters.—Carapace depressed, regions well defined, with depressed coarse granulations on anterior and anterolateral portions, an oblique ridge on hepatic region. Five anterolateral teeth with granulate margins; second tooth small, blunt, obsolescent in young but considerably larger than first in adults; third and fourth teeth large, acute; fifth tooth small and pointed. Front slightly deflexed, shallow, lobes separated by a narrow fissure; margin sinuous, outer corner rectangular. A slight subhepatic elevation formed by a number of granules.

Chelipeds rugose with coarser granules than on carapace; merus with a row of spines above; carpus with a deep distal groove and two inner spines, one above other, upper one largest. Chelae roughened proximally and on upper portion, roughness more extensive on minor chela; fingers deeply grooved, major dactyl with large basal tooth. Walking legs long, slender; merus with row of spines above, other articles spinulose.

Measurements.—Carapace: male, length, 7 mm.; width, 10 mm.

Color.—"Anterior portion of carapace light yellowish orange. Fingers of major chela brownish black, of minor chela black. Spines and tu-

bercles of both chelipeds light salmon." (Rathbun, 1930a.)

Habitat.—Various types of bottom in deeper water; 7.5 to 182 fathoms.

Type locality.—Off Grenada.

Known range.—Cape Hatteras, N.C.; Florida through Gulf of Mexico and West Indies to Cabo Frio, Rio de Janeiro, Brazil; Yucatan.

Remarks.—Ovigerous females are known in June and August from Florida, and in October from North Carolina (Rathbun, 1930a, in part).

Micropanope nuttingi (Rathbun)

Figures 177, 183J

Xanthias nuttingi Rathbun, 1898, p. 271, pl. 4, fig. 1.
Micropanope nuttingi: Rathbun, 1930a, p. 450, fig. 74 (rev.).

Recognition characters.—Carapace suboval, convex from front to back, nearly flat transversely; regions distinct, anterior half rough with squamose tubercles. Second normal anterolateral tooth completely united with small first tooth; three remaining teeth sharp pointed, posterior one smallest. Front convex, bilobulate, with granulate margins separated by a V-shaped sinus, outer angle of each lobe subrectangular.

Chelipeds heavy, quite unequal; merus spinulose on upper edge; carpus covered with beadlike tubercles, with a deep distal groove, and an inner angular eminence tipped with a spinule and a second spinule below. Females with whole outer surface of both chelae tuberculate. Major chela of males with upper and approximately two-thirds of outer surface beaded, tuberculate; lower third and distal extremity smooth and shining; fingers broad, not gaping, brown with light tips, color of immovable finger not continued on palm and ending in a line with articulation of dactyl; dactyl with large basal tooth. Minor chela almost entirely tuberculate, growing less so toward distal and lower margins; upper margin with longitudinal groove, fingers deeply grooved. Upper margin of walking legs tuberculate or granulate.

Measurements.—Carapace: male, length, 4 mm.; width, 6 mm.

Color.—"In alcohol, speckled with blue; larger patches of blue on anterior gastric and cardiac region." (Rathbun, 1930a.)

Habitat.—Has been taken from boulder-covered beach, from *Porites* clumps and *Halimede* (U.S. National Museum records); shallow water to 100 fathoms.

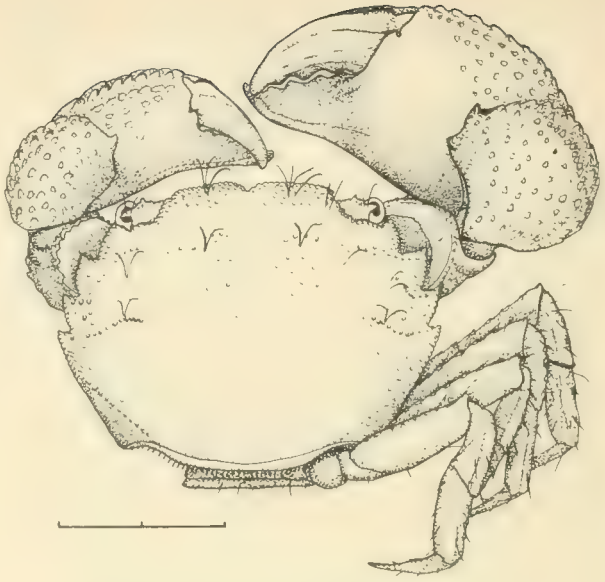

FIGURE 177.—*Micropanope nuttingi* (Rathbun). Animal in dorsal view, walking legs of left side not shown. 2 mm. indicated.

Type locality.—Bahama Banks.

Known range.—Cape Hatteras, N.C., through Gulf of Mexico and West Indies to Cape São Roque, Rio Grande do Norte, Brazil.

Remarks.—Ovigerous females have been taken in July in Florida.

Genus ***Eurypanopeus*** Milne Edwards, 1880

Rathbun, 1930a, p. 403.

KEY TO SPECIES IN THE CAROLINAS

a. Fingers of both chelae with acute tips, not spooned *abbreviatus* (p. 194).

aa. Fingers of minor chela spoon-shaped at tip *depressus* (p. 195).

Eurypanopeus abbreviatus (Stimpson)

Figures 178, 183K

Panopeus abbreviatus Stimpson, 1860a, p. 211.
Eurypanopeus abbreviatus: Rathbun, 1930a, p. 404, text-fig. 63, pl. 172, figs. 1–2 (rev.).

Recognition characters.—Carapace approximately two-thirds broader than long, moderately convex in two directions, naked above, granulate and uneven on front and along anterolateral border, smooth and polished elsewhere; areolations slightly but distinctly indicated, a number of well-marked rugae among granules. Front strongly deflexed, four-lobed, median lobes prominent, separated by a V-shaped notch. Antero-

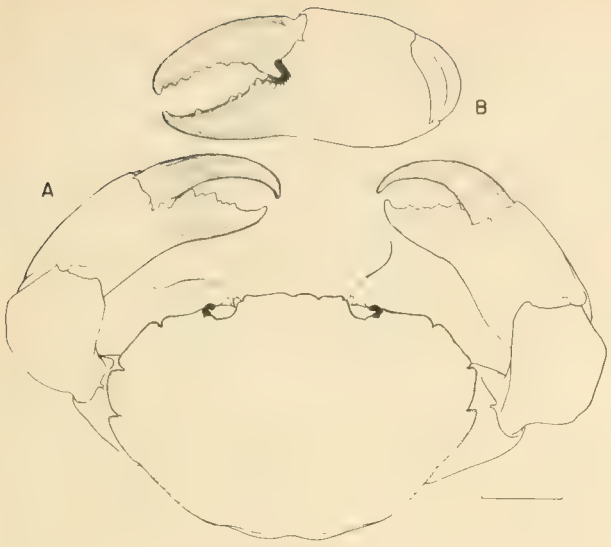

FIGURE 178.—*Eurypanopeus abbreviatus* (Stimpson). A, male in dorsal view, walking legs not shown; B, right chela in frontal view; front with anomalous notch to right of midline; 5 mm. indicated.

lateral margin thin, divided into four lobes, first and second teeth coalesced, separated by a slight concavity; third tooth obtuse; fourth with outer margin longitudinal or nearly so; fifth subtriangular, directed outward. A low granulated swelling below interval between first two teeth.

Chelipeds quite unequal in males; carpus with blunt internal tooth; fingers slender, pointed, widely gaping in major chela; fitting closely in minor, tips crossing in both; major dactyl with a large basal tooth, color of fingers not extending on palm.

Measurements.—Carapace: male, length, 14 mm.; width, 22 mm.

Color.—Yellowish or brownish above, front margin of carapace and chelipeds roseate or tinged with bluish purple; fingers black with paler tips. Brazilian specimens with a number of large dark spots on upper half of chelipeds.

Habitat.—Specimens have been found near shore on oysterbeds, under rocks, and among sponges and bryozoan growth; shore and shallow water to unknown depth.

Type locality.—Barbados, British West Indies.

Known range.—South Carolina, through West Indies and Gulf of Mexico to State of Santa Catarina, Brazil.

Remarks.—Ovigerous females are known from April to November in the West Indies, and August to November in southern Brazil (Rathbun, 1930a, in part).

Eurypanopeus depressus (Smith). Flat mud crab

Figures 179, 183L

Panopeus depressus Smith, 1869a, p. 283.

Eurypanopeus depressus: Hay and Shore, 1918, p. 437, pl. 34, fig. 4.—Rathbun, 1930a, p. 410, text-fig. 65, pl. 173, figs. 3–4 (rev.).

Recognition characters.—Carapace transversely oval, approximately three-fourths as long as wide, flattened posteriorly, convex in anterior half; areolations well defined, finely granulate, with several pairs of transverse rows of granulations. Anterolateral teeth four, outer margins granulate; first two teeth coalesced to form broad lobe with slightly sinuate margin; third tooth blunt; fourth and fifth spines tipped, pointing obliquely upward and forward. Front nearly straight, median notch small or absent.

Chelipeds dissimilar and quite unequal. Smaller one more rugose than larger and with margins of fingers nearly straight and opposable for a considerable distance, with opposed margins of tips thin edged and hollowed out—"spoon shaped." Larger cheliped with nearly smooth articles, hand heavy and inflated; dactyl strongly curved, obscurely toothed at base, and meeting immovable finger only at tip; internal tooth of carpus tipped with small spinule; in unworn condition both fingers show indication of spoonlike flattening.

Measurements.—Carapace: length, 14 mm.; width, 20 mm.

Variations.—Ryan (1956) described a persistent, central, oval, blood-red spot or structure on the inner surface of the ischium of the third maxillipeds of both sexes. The spot is often two-thirds the length of the article, with its surface raised slightly above the surface of the ischium. When pressure is applied, the hard spot cracks and is easily dissected out. A similar spot has been noted on *P. herbstii.*

The normal male abdomen is narrow with the third, fourth, and fifth segments fused. A few variant males have wide abdomens with seven segments, resembling females.

Color.—Mottled grayish olive or dark olive brown, especially on upper surfaces of chelipeds and anterior portions of carapace; fingers dark brown with dark color of immovable finger extended on palm; body and legs light colored underneath.

FIGURE 179.—*Eurypanopeus depressus* (Smith). A, animal in dorsal view, walking legs not shown; B, large chela in frontal view; 5 mm. indicated.

Habitat.—In Chesapeake Bay, Ryan (1956) found this species in greater abundance on oyster bars than any other species of mud crab, and evidence was presented showing a positive relationship between presence of oyster shells and this species. Others have noted a similar habitat preference (Lunz, 1937a). In the bay, the depth range was 1 to 15 fathoms (Cowles, 1930, in part), and the salinity range occupied was 4.5 to 20.4 ‰. Elsewhere the species occurs from shore to 26 fathoms.

Type locality.—New Haven, Conn.

Known range.—Massachusetts Bay through Florida (east and west coasts) to Texas; Bermuda; West Indies.

Remarks.—Ryan (1956) gave much detail on the life history of this species in Chesapeake Bay. Ovigerous females were collected from June to September. Elsewhere, Rathbun (1930a) and Lunz (1937a) reported such females in April from Virginia and South Carolina, September from Mississippi and the Leeward Islands, November and February from Florida. Zoeal stages have been studied by Hyman (1925) from plankton tows made in the Beaufort, N.C., area. Costlow and Bookhout (1961b) worked out the entire larval and postlarval history in captivity and illustrated four zoeal stages and a single megalops stage. Immature males from Chesapeake Bay ranged in width from 3.2 to 6 mm. and females from 3.6 to 6.4 mm.

Maturity was considered to be attained at widths of 5.1 to 6 mm. in males, and 5.5 to 6.4 mm. in females. The mature individuals range widely in size, up to a width of 21 mm. for females, and ovigerous females show a range of 6 to 17 mm. Such a broad range of sizes among mature individuals suggested to Ryan that growth and molting continue after maturity is reached. Maturity may be reached in the first summer after eggs have hatched.

McDermott (1960) found that *E. depressus* is a predator on oyster spat in southern New Jersey but not so serious a pest as *P. herbstii.*

Genus ***Panopeus*** H. Milne Edwards, 1834

Rathbun, 1930a, p. 333.

KEY TO SPECIES IN THE CAROLINAS

a. Dark color of immovable finger continued more or less on outer surface of palm, especially in males; no distal groove on carpus of chelipeds.....*herbstii* (p. 196).

aa. Dark color of immovable finger not continued on outer surface of palm; carpus of chelipeds with shallow groove parallel to distal margin..*occidentalis* (p. 198).

Panopeus herbstii H. Milne Edwards. Common mud crab

Figures 180, 183M

Panopeus herbstii H. Milne Edwards, 1834, p. 403.—Hay and Shore, 1918, p. 437, pl. 34, fig. 9.—Rathbun, 1930a, p. 335, text-figs. 52–53, pl. 156, figs. 1–3; pl. 157, figs. 1–3 (rev.).

Recognition characters.—Carapace approximately two-thirds as long as wide, regions well marked, surface sparingly granulate. Anterolateral margins with five teeth; first two teeth coalescent; third and fourth larger, prominent, and with arcuate outer margins and acute tips; fifth smaller, acute at tip and with outer margin straight. A transverse ridge extending inward from fifth tooth, and a shallow groove from fourth tooth. Front wide, not produced, with narrow median fissure; anterior margin of each half sinuous. Male abdomen with sides of

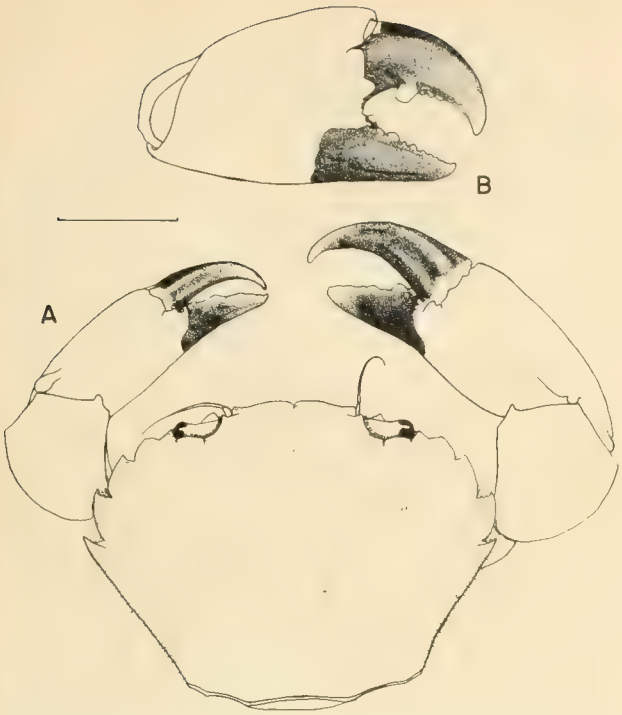

FIGURE 180.—*Panopeus herbstii* H. Milne Edwards. A, animal in dorsal view, walking legs not shown; B, right chela in frontal view; 5 mm. indicated.

penultimate segment nearly parallel; terminal segment broader than long, rounded at tip.

Chelipeds heavy, finely granulate; carpus without groove on superior surface and with a blunt internal spine; hands unequal and dissimilar, large one with dactyl curved and strongly toothed at base, dactyl of smaller more nearly straight; fingers dark, with color extending somewhat on palm.

Measurements.—Carapace: male, length, 26 mm.; width, 38 mm.

Variations.—Rathbun (1930a) separated this species into a number of forms on the basis of structural characteristics but considered these the result of response to environment rather than genetic differences. Intermediates may occur in any locality; thus, the forms are not always easily separated.

Ryan (1956) described a persistent, central, oval, red spot or structure on the inner surface of the ischium of the third maxillipeds of both sexes. Mrs. Peggy Keney of the U. S. Fish and Wildlife Service Bureau of Commercial Fisheries, Biological Laboratory, Beaufort, N.C., found this spot to occur on 100 percent of males and 55 percent of females in the Beaufort area. A sample of 596 specimens was examined.

Habitat.—Depth distribution for the species ranges from the intertidal zone to 12 fathoms. Ryan (1956) found the species to be rare in Chesapeake Bay in a salinity range of 13.95 to 19.04‰. The depth distribution there was 2 to 6 fathoms and at each collection spot the bottom was composed of soft mud with few oyster shells. McDermott and Flower (1953) found the species common on oyster beds in Delaware Bay, where it commonly cracks and eats small oysters and the barnacle *Balanus eburneus*. The toadfish was considered a common predator.

In North Carolina and South Carolina, this is one of the most common crabs of estuarine regions, found wherever the bottom is muddy or covered with shells or stones. In some localities along edges of the higher marshes, it is found in burrows and is frequently associated with *Sesarma reticulata* and *Uca minax*.

In the West Indies, collections have been made from mangrove roots, sponges, and coral reefs.

Type locality.—North America.

Known range.—Boston, Mass., to State of Santa Catarina, Brazil; Bermuda.

Remarks.—This common xanthid crab has a fossil record dating from the Miocene in North America, and the genus *Panopeus* has a record extending from the Eocene to the present (Rathbun, 1935).

Ovigerous females are known virtually the year around in Florida. They are known through late spring and summer in the Carolinas, in July in Maryland, February to September in various parts of the West Indies, and August to October in southern Brazil.

Ryan (1956) gave carapace widths of mature males as 8.3 to 37.3 mm., and of mature females as 21.6 to 27.8 mm. A specimen 45 mm. wide was found at Beaufort, N.C., in 1960 (Mrs. Keney, personal communication), and Wass (1955) reported a male 55 mm. wide.

Costlow and Bookhout (1961a) reviewed early descriptions of larvae and described and illustrated four zoeal and one megalops stage reared in the laboratory.

Costlow, Bookhout, and Monroe (1962) reared the larval stages under 12 different conditions of

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salinity and temperature. Eggs were maintained in salinities of 12.5, 20.1, 26.5, and 31.1 °/₀₀ and all larvae hatched as first stage zoeae. Succeeding stages showed higher percentages of survival under different conditions, with shortest development time in the highest salinity. The lowest salinity tested did not permit development to be completed. In addition, low temperature affected duration of all larval stages and mortality of some stages. Larval development was completed to first crab in 48–52 days at 20° C., in 18–28 days at 30° C. From data, the effects of salinity and temperature on mortality of larval stages were projected by statistical methods over a wide range of combinations. The hypothesis is presented that the effect of temperature on successive larval stages limits the productive spawning period. Low temperatures favor the spring brood of larvae [in these latitudes], prolonging larval development until warmer water produces favorable conditions for the megalops stage. Larvae hatched in fall are not so favored and mortality in late zoeal and megalops stages would be high.

In a study of the relationship of habitat to oxygen consumption by estuarine crabs, Ayers (1938) found *P. herbstii* to be intermediate in a scale of partial adaptation of the respiratory mechanisms to life in air. Teal (1959) found this species active on Georgia marshes when the tide was high or the sky cloudy. When the marsh was exposed, it was found in burrows, usually near the top, in air or water. Among various marsh crabs studied (see remarks, *Uca minax*) only *P. herbstii* was active at temperatures below 12° C. Respiration in this crab was most affected by reduced oxygen pressure among species tested, showing a rate reduction of 90 percent at 4 mm. Hg.

Menzel and Nichy (1958) found that *P. herbstii* and *Menippe mercenaria* are the only xanthids large enough to kill significant numbers of adult oysters. McDermott (1960), studying predatory activities of xanthid crabs on oyster beds in New Jersey, found that *P. herbstii* destroyed 1- and 2-year-old oysters at a rate of 0.15 oysters per crab per day. The crab also preyed actively on oyster spat as well as barnacles (*Balanus improvisus*). He concluded that *P. herbstii* is potentially the most destructive of the five species of mud crabs occurring on New Jersey oyster beds.

Panopeus occidentalis Saussure

Figures 181, 183N

Panopeus occidentalis Saussure, 1857, p. 502.—Rathbun, 1930a, p. 348, text-fig. 55; pl. 161, figs. 1–3 (rev.).

Recognition characters.—Similar to *Panopeus herbstii*, but differing in having more convex carapace, especially in gastric region; front narrow, advanced; second anterolateral tooth usually narrower and separated by deeper sinus from first tooth, third to fifth teeth thicker, more prominent and widely separated, third one blunt, forming almost a right angle at tip; abdomen of male wider, sides of penultimate segment not parallel, narrowed toward proximal end.

Carpus of chelipeds with groove parallel to distal margin, sometimes rugose; dark color of immovable finger not continued on palm. Walking legs somewhat longer and more slender.

Measurements.—Carapace: male, length, 23 mm.; width, 33 mm. Smaller than *P. herbstii*.

Variations.—There is considerable variation even in a single lot of specimens. The carapace may be smooth and shining, or with light, granulate, transverse lines; the second anterolateral tooth may be small, subacute, and similar to the first rather than broadly rounded and large; the female abdomen may have sides of the sixth segment parallel instead of converging slightly toward the proximal end. Variations in teeth of the anterolateral border were noted in 12 percent of females studied by de Oliveira (1940). In these the first, second, and third teeth of one side were depressed, giving the impression of but one sinuous tooth while those of the other side were normal.

This species, like *P. herbstii*, has been divided into two environmental forms (typical and serrate), and both occur in the Carolinas (Rathbun, 1930a).

Color.—Carapace dull yellow spotted with brown and red; legs yellow with brown maculations and speckles on chelipeds; walking legs with brown or rose streaks. De Oliveira (1940) gave color of the species in Brazil as: carapace dark yellow with red blotches or chocolate varying in tone; legs same color but spotted with reticulated points, points of fingers chocolate to almost black; body yellow ventrally, legs yellow to grayish; some rare specimens completely yellow.

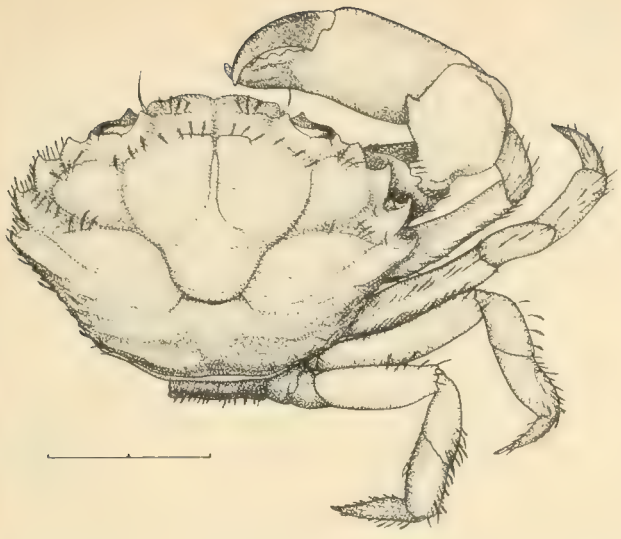

FIGURE 181.—*Panopeus occidentalis* Saussure. Animal in dorsal view, legs of left side not shown, 10 mm. indicated.

Habitat.—This species has been found among rocks, mangrove roots, sponges, ascidians, and seaweed, and on pilings of piers along shore; shore to 10 fathoms.

Type locality.—Guadeloupe.

Known range.—North Carolina to State of Santa Catarina, Brazil; West Indies and Bermuda.

Remarks.—De Oliveira (1940) reported in some detail on the natural history of this species where it occurs in the vicinity of the Ilha Pinheiro, near Rio de Janeiro, Brazil. The species is primarily crepuscular or nocturnal and is found living chiefly in ditches, between and beneath stones, and among mangrove roots, often burrowing to a depth of 30 cm. Both sexes were found together except when the eggs were deposited, and then females were not so often seen. Molting individuals and copulating pairs were rarely found.

Mating pairs were found from November to December, and on one occasion in water of 22 ‰ at 22° C. Periods of egg deposition extended from January to May, and again from July to August (September, Rathbun, 1930a). (In the Caribbean area ovigerous females are known from January to July, U.S. National Museum records.) The seldom-seen ovigerous females bore dark, chocolate colored eggs. Such females showed a range in carapace width from 13.3 mm. to 35.2 mm., and bore 3,000 to 70,000 eggs, depending on size. Females were observed to aerate and clean the eggs in water at low tide in the evening. Eggs in the laboratory hatched in about 15 days. Molting of females followed hatching of eggs.

Young of the species were found throughout the year, as others have noted. One large male measured 48.2 mm. [width], though the average dimension for the typical form was 27.7 mm. long by 40.5 mm. wide; for the serrate form, 19.9 mm. long by 27.5 mm. wide.

The species was believed to have few natural enemies. Material from the gut was found to consist of a variety of plant and animal matter. In addition to the ecological discussion, de Oliveira gave a number of observations on autotomy and its effect on movement and behavior.

Genus ***Eurytium*** Stimpson, 1859

Rathbun, 1930a, p. 422.—Hemming, 1958b, p. 32.

Eurytium limosum (Say)

Figures 182, 183 O

Cancer limosa Say, 1818, p. 446.

Eurytium limosum: Hay and Shore, 1918, p. 438, pl. 35, fig. 7.—Rathbun, 1930a, p. 423, pl. 176, figs. 1–2 (rev.).

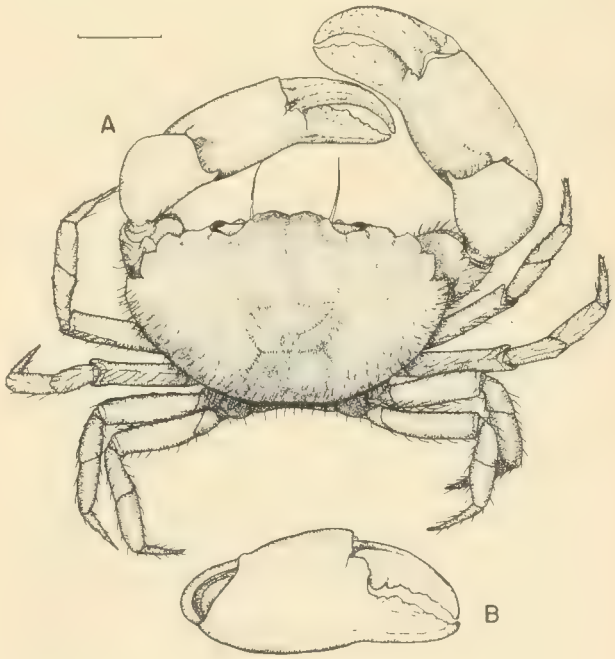

FIGURE 182.—*Eurytium limosum* (Say). A, animal in dorsal view; B, large chela in frontal view; 10 mm. indicated.

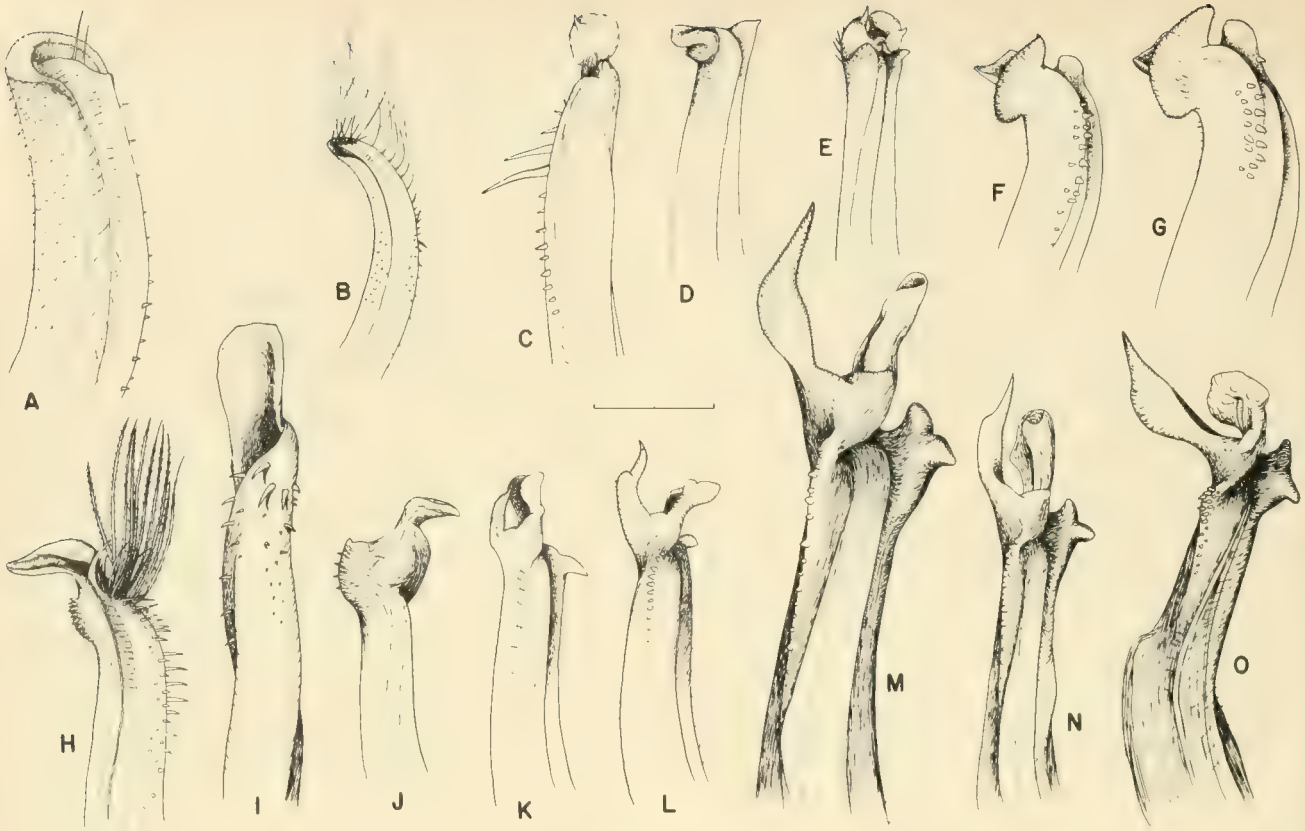

FIGURE 183.—Tips of right first pleopods of male xanthids; A, *Glyptoxanthus erosus* (Stimpson), medial view; B, *Carpoporus papulosus* Stimpson, medial view; C, *Rhithropanopeus harrisii* (Gould), medial view; D, *Hexapanopeus angustifrons* (Benedict and Rathbun), medial view; E, *Hexapanopeus paulensis* Rathbun, medial view; F, *Neopanope texana texana* (Stimpson), medial view; G, *Neopanope texana sayi* (Smith), medial view; H, *Leptodius agassizii* Milne Edwards, medial view; I, *Micropanope xanthiformis* (Milne Edwards), abdominal view; J, *Micropanope nuttingi* (Rathbun), medial view; K, *Eurypanopeus abbreviatus* (Stimpson), medial view; L, *Eurypanopeus depressus* (Smith), medial view; M, *Panopeus herbstii* H. Milne Edwards, medial view; N, *Panopeus occidentalis* Saussure, medial view; O, *Eurytium limosum* (Say), medial view; 0.5 mm. indicated for all figures, except I and J twice this magnification, and O one-half this magnification.

Recognition characters.—Carapace broad, approximately 1.5 times as wide as long, quite convex from front to back, nearly plane from side to side; surface smooth to eye but under a lens finely granulate, granulations coarser near frontal and anterolateral margins. Front approximately one-fourth width of carapace, divided into two lobes by a median notch giving rise to a shallow groove disappearing over gastric region. Orbital margins somewhat elevated; external orbital tooth coalesced with first tooth of anterolateral border, division between these teeth indicated by a shallow notch. Anterolateral teeth with raised margins, second and third teeth rounded at tip, fourth more prominent and subacute.

Chelipeds massive, unequal, and dissimilar, more so in male than in female; merus with coarsely tuberculate superior border and a distal spiniform tooth; carpus with a narrow internal spine, not grooved; fingers pointed, deflexed, with large basal tooth on major dactyl.

Measurements.—Carapace: length, male, 24 mm.; width, 36 mm.

Color.—Carapace brilliant purplish blue, dark gray, or black; carpus and hand bluish; proximal upper half of dactyl pink or purple; remainder of fingers porcelain white; lower portion of chelipeds, and also carpal teeth, yellow or orange; color of fingers not continued on palm.

Habitat.—This primarily tropical species lives in muddy or marshy banks a bit below the high-

tide mark in burrows partially filled with water, among stones at the high-tide mark, in burrows in sand, under stones between tides, and on coral reefs (Rathbun, 1930a). High-tide mark to shallow depths near shore.

Type locality.—"Inhabits shores of the Northern States."

Known range.—Modern records, South Carolina to State of São Paulo, Brazil; Bermuda. Formerly reported from New Jersey (Ryan, 1956).

Remarks.—This species has a fossil record in North America dating from the Miocene of North Carolina and Florida (Rathbun, 1935).

Teal (1959) found this species active on Georgia marshes when the tide was high or the sky cloudy. When the marsh was exposed, it was found in burrows, usually near the top, either in air or water. Respiration rates in water were higher than in air. The species showed internal regulation of metabolism in that it was independent of oxygen tension but not of acclimation to temperature.

Ovigerous females have been reported from Florida in August (Wass, 1955).

Family **Goneplacidae**

Palp of external maxillipeds articulating at or near anterointernal angle of merus; exognath normal in size, not concealed. Antennular septum a thin plate. Division of orbit into two fossae usually not indicated. Genital ducts of male usually perforating base of last pair of legs, often passing through a groove in sternum.

This group has a general resemblance to the Xanthidae in body shape. Members of the group are all bottom dwellers.

KEY TO GENERA AND SPECIES IN THE CAROLINAS

a. Base of third segment of male abdomen covering whole space between last pair of legs; carapace subquadrate, widest between postorbital angles; anterior border entirely occupied by square-cut front, and orbits formed into long, narrow trenches—*Goneplax hirsuta* (p. 201).

aa. Base of third segment of male abdomen not covering whole space between last pair of legs.

b. Frontoorbital width almost as great as total width of carapace; eyestalks long; carapace subquadrate, posterolateral margins converging *Euryplax nitida* (p. 202).

bb. Frontoorbital width from one-half to three-fourths total width of carapace; eyestalks short; anterolateral margins arcuate *Speocarcinus carolinensis* (p. 202).

Genus ***Goneplax*** [Leach, 1814]

Rathbun, 1918b, p. 25.—Hemming, 1958a, p. 32.

Goneplax hirsuta Borradaile

Figure 184

Goneplax hirsuta Borradaile, 1916, p. 99, fig. 11.—Rathbun, 1918b, p. 28, text-fig. 7 (rev.).

Recognition characters.—Carapace approximately two-thirds as long as broad, greatest width between tips of postorbital spines; regions faintly marked except for H-shaped depression in middle. Sides converging backward from prominent, sharp, postorbital spines; armed with sharp spine near postorbital spine. Front almost straight, with low rostral prominence in broad, shallow median notch. Orbital margin sinuous, sloping backward, width of orbit and front nearly equal.

Chelipeds almost equal; merus about two-thirds length of carapace, deep, with a spine a little beyond middle of upper edge; carpus broader than long, with a stout internal spine. Hand longer than remainder of limb; fingers about equal to palm, irregularly toothed, not gaping; external base of hand and distal half of carpus with a long dense tuft of hair, fringe of similar hairs along inner side of merus. Walking legs slender, meri smooth or fringed with light pubescence, distal articles fringed with hairs.

Measurements.—Carapace: male, length, 19 mm.; width, 29 mm.

Habitat.—Forty to eighty fathoms.

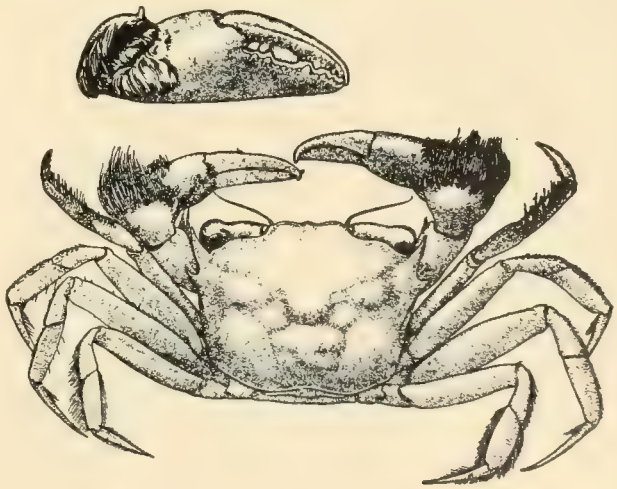

FIGURE 184.—*Goneplax hirsuta* Borradaile. A, animal in dorsal view; B, right chela and carpus in outer view; approximately × 1.75 (after Borradaile, 1916).

Known range.—North Carolina to Rio de Janeiro, Brazil.

Remarks.—Ovigerous females have been taken in the Gulf of Mexico off Florida in June (U.S. National Museum records).

Genus ***Euryplax*** Stimpson, 1859

Rathbun, 1918b, p. 34.—Hemming, 1958b, p. 32.

Euryplax nitida Stimpson

Figure 185

Euryplax nitida Stimpson, 1859, p. 60.—Rathbun, 1918b, p. 34, text-fig. 11, pl. 7 (rev.).

Recognition characters.—Carapace smooth and shining, convex. Front deeply notched on each side at insertion of antennae; interantennal margin nearly straight. Anterolateral margins converging anteriorly, less than half as long as posterolateral margins and armed with three strong teeth including outer orbital. Carapace widest at level of third tooth.

Merus of chelipeds in male with a deep round pit at anterior distal corner of lower surface, pit surrounded by a fringe of long hair, and with a sharp curved spine near distal end of upper surface; carpus with a sharp inner spine and inner surface pilose. Walking legs slender.

FIGURE 185. *Euryplax nitida* Stimpson. Male in dorsal view, legs of left side not shown. 5 mm. indicated.

Female with narrower carapace; chelipeds more nearly equal, and merus lacking pit with surrounding hair.

Measurements.—Carapace: male, length, 15 mm.; width, 25 mm.

Color.—Distal half of fingers white (Rathbun, 1918b).

Habitat.—Shallow water to 49 fathoms.

Type locality.—Florida Keys.

Known range.—Off Beaufort, N.C., to Texas; West Indies to St. Thomas; Bermuda.

Remarks.—Ovigerous females have been taken in June from southern Florida.

Genus ***Speocarcinus*** Stimpson, 1850

Rathbun, 1918b, p. 38.—Hemming, 1958b, p. 37.

Speocarcinus carolinensis Stimpson

Figure 186

Speocarcinus carolinensis Stimpson, 1859, p. 59, pl. 1, figs. 1–3.—Rathbun, 1918b, p. 39, pl. 8, pl. 159, fig. 6 (rev.).

Recognition characters.—Carapace subcylindrical, nearly smooth, punctate, obscurely granulate near margins, pubescent; gastric region and subdivisions well defined. Anterolateral margin with five teeth including outer orbital; second tooth rounded and not always separated from first; last three teeth sharp, well defined. Posterolateral margins parallel. Front approximately one-fourth width of carapace, sinuous, nearly straight, with median emargination. Eyestalks constricted near cornea.

Chelipeds strong, nearly smooth, margins hairy; merus with a strong spine on upper border; carpus granulate internally and with a blunt internal tooth; hand with outer surface smooth, microscopically granulate; dactyl with stout tooth at base. Walking legs with hairy margins.

Measurements.—Carapace: male, length, 23 mm., width, 29 mm.; female, length, 17 mm., width, 27 mm.

Habitat.—"This crab lives in the subterranean galleries excavated in the mud at low-water mark by the *Squilla*, *Callianassa*, and other Crustacea, or by large worms," (Stimpson *in* Rathbun, 1918b); near low-tide mark to 76 fathoms.

Type locality.—Charleston Harbor, S.C.

Known range.—South Carolina through Gulf of Mexico and West Indies to Surinam.

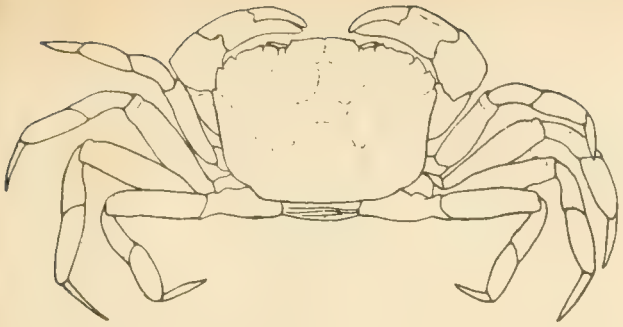

FIGURE 186.—*Speocarcinus carolinensis* Stimpson. Type female in dorsal view (after Rathbun, 1933).

Family **Pinnotheridae**

Carapace often somewhat membranous. Anterolateral margins entire or very slightly dentate. Front, orbits, and eyestalks very small, cornea often rudimentary. Buccal cavity usually wide, often semicircular in outline. Merus of third maxilliped never quadrate, and never with palp distinctly at anterointernal angle; ischium small, absent, or fused with merus and directed obliquely inward (Rathbun, 1918b).

Small crabs living as commensals or parasites in bivalve mollusks, ascidians, worm tubes, and on or in echinoderms. Free living or migratory stages are occasionally taken in open water.

KEY TO GENERA IN THE CAROLINAS

a. Dactyls of walking legs simple, acute.
  b. Third walking leg little, if any, longer than other legs.
    c. Carapace suborbicular and somewhat membranous in mature female, flattened and firm in hard stage male and female buccal mass subquadrate *Pinnotheres* (p. 203).
    cc. Carapace oval, flattened, and rather firm; buccal mass subtriangular *Parapinnixa* (p. 208).
  bb. Third walking leg longer and stronger than others, often considerably so *Pinnixa* (p. 210).
aa. Dactyls of first, second, and third walking legs bifurcate *Dissodactylus* (p. 209).

Subfamily **Pinnotherinae**

Carapace usually not markedly transverse. Ischium of external maxillipeds either rudimentary or indistinguishably fused with merus to form single piece, usually oblique, occasionally nearly transverse; palp not so large as merus-ischium (Rathbun, 1918b).

Genus *Pinnotheres* Bosc [1801 or 1802]

Rathbun, 1918b, p. 62.—Hemming, 1958b, p. 36.

KEY TO SPECIES IN THE CAROLINAS

Hard-stage males and females

a. Carapace with a striking pattern of light spots on dark background of pubescence *maculatus* (p. 206).
aa. No striking color pattern *ostreum* (p. 203).

Posthard females (and male *maculatus*)

a. Carapace nearly naked *ostreum* (p. 203).
aa. Carapace covered with a short deciduous pubescence *maculatus* (p. 206).

Pinnotheres ostreum Say. Oyster crab

Figures 187, 188, 189

Pinnotheres ostreum Say, 1817, p. 67, pl. 4, fig. 5.—Rathbun, 1918b, p. 66, text-fig. 30; pl. 15, figs. 3–6 (rev.).—Hay and Shore, 1918, p. 443, pl. 35, fig. 9.

Pinnotheres depressum Say, 1817, p. 68.

Pinnotheres depressus: Rathbun, 1918b, p. 79, pl. 17, figs. 1–2 (rev.).

Recognition characters.—Mature female: Carapace subcircular in outline; surface glabrous for most part, smooth, shining, membranous, yielding to touch, convex from front to back and with a broad, shallow, longitudinal depression at each side of cardiac and gastric areas. Lateral margins thick and bluntly rounded; posterior margin broad. Front rounded, slightly produced, covering and concealing eyes. Orbits small, subcircular, anteriorly placed. Antennule large; antenna small, flagellum not so long as diameter of orbit. Buccal mass roughly quadrangular in outline but bent into broad crescentic arch, short anteroposteri-

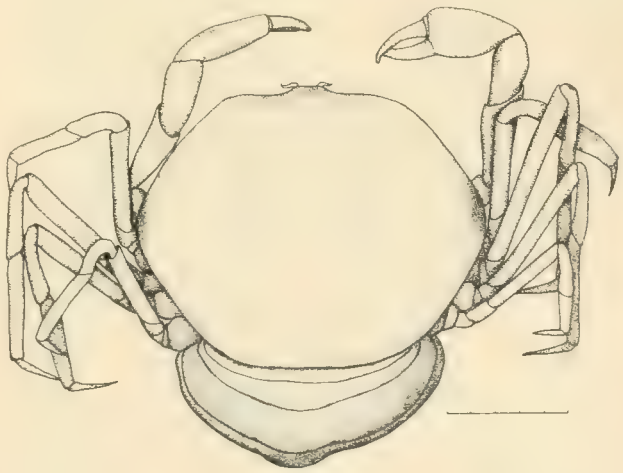

FIGURE 187.—*Pinnotheres ostreum* Say. Mature female in dorsal view, 5 mm. indicated.

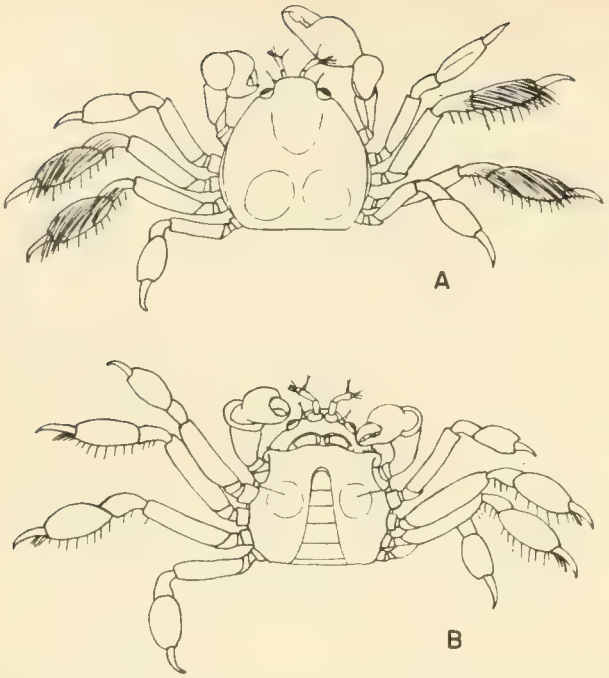

FIGURE 188.—*Pinnotheres ostreum* Say. A, stage I female in dorsal view; B, stage I female in ventral view; approximately × 9 (after Stauber, 1945).

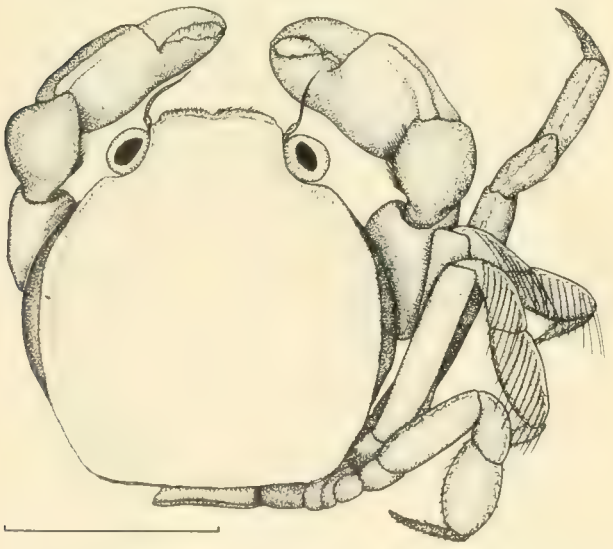

FIGURE 189.—*Pinnotheres ostreum* Say. Male in dorsal view, walking legs of left side not shown, 1 mm. indicated.

orly. Outer maxilliped with ischium and merus fused; carpus, or first article, of palp short, oblong; propodus elongate, end rounded; dactyl inserted behind middle of propodus, minute, slender.

Chelipeds small; merus and carpus rather slender. Palm somewhat flattened inside, swollen outside, strongly widened from proximal toward distal end, then narrowed; width across base of fingers less than greatest width of palm; fingers, especially immovable one, stout, not gaping, tips hooked past each other, minute teeth on opposed edges, a larger tooth near base of each, immovable finger horizontal. Walking legs slender, subcylindrical; last two articles with thin fringe of hair; second and third legs about equal in length, first legs slightly stouter, last pair turned backward and upward.

Abdomen large, extending beyond carapace in all directions.

Measurements.—Carapace: width, ranging from 4 to 15 mm. (Christensen and McDermott, 1958).

Color.—Whitish or salmon pink.

Recognition characters.—Mature male and hard-stage female: Carapace well calcified, flat dorsally, subcircular in outline, with truncate front more advanced than in mature female. Posterior margin straight; lateral margin thin, rather sharply bent from dorsal side, margin marked by a raised band of short dense hair. Eyes well developed. Buccal mass crescentic, arched, broad from side to side but short anteroposteriorly; cavity completely closed by external maxillipeds formed as in mature female.

Chelipeds stout; merus and carpus not slender as in mature female. Palm slightly flattened inside, swollen outside, and shaped as in mature female, both margins convex. Hand with bands of pubescence on upper and outer surface of palm, and outer surface of immovable finger. Fingers stout, especially immovable finger, with tips hooked past each other when closed; dactyl with small tooth proximally, tooth fitting between two protuberances on immovable finger when closed; both fingers with stiff hairs on gripping edges. Walking legs flattened, with posterior margins thickened, and with plumose swimming hairs on second and third pairs.

Abdomen narrow, confined to sternal depression; copulatory stylets of male well developed, first pair bladelike and hairy, second pair rodlike and almost hairless (Stauber, 1945).

Measurements.—Carapace: male, width, 1.4 to 4.6 mm.; female, width, 1.3 to 2.7 mm. (Christensen and McDermott, 1958).

Color.—Dark or medium-dark brown with two large, distinct, almost circular, pale white spots on both carapace and sternum; dorsal spots on branchial regions, ventral spots flanking abdomen and medial to first pair of legs; color and spots persistent in alcohol (various authors).

Habitat.—Parasitic [or commensal] chiefly in the oyster, *Crassostrea virginica*, also in *Pecten* spp. and *Anomia simplex* (Christensen and McDermott, 1958), and in *Mytilus edulis* (McDermott, 1961). Also occasionally found in *Chaetopterus* tubes (Gray, 1961).

Type locality.—Given as—"inhabiting the common oyster."

Known range.—Salem, Mass., to State of Santa Catarina, Brazil.

Remarks.—Say's *P. depressus* appears almost certainly to be the hard-stage male as described above and discussed below.

The works of Hyman (1924a), Stauber (1945), Sandoz and Hopkins (1947), and Christensen and McDermott (1958) together have made knowledge of the biology and life history of *P. ostreum* the most complete for any species of *Pinnotheres* in the world. The serious student should refer to these thorough works, for they can be summarized only in barest outline here. The complex life cycle of this species encompasses many developmental stages, as well as a striking sexual dimorphism in the mature animals, which, together with the structural specializations and mode of existence, demonstrate a beautiful accommodation to an unusual habitat.

The larval stages include four zoeae followed by one megalops. The first two zoeal stages were described by Hyman (1924a), and a description of all these stages (partial for fourth zoeal stage) was given by Sandoz and Hopkins (1947). In general, the zoeae and megalops have no dorsal or lateral spines on the carapace. Time of development from hatching to molting of the megalops to first crab stage is 25 days.

From the first crab stage on, development is summarized by Christensen and McDermott (1958, p. 154). The first crab stage, actually the stage which invades oysters, is called the invasive stage by these authors. It was described by Sandoz and Hopkins (1947) and in many respects is similar to the later hard stage in its flattened shape, legs adapted for swimming, and characteristic color markings (carapace width, 0.59–0.73 mm.).

In Delaware Bay, few invasions take place before August 1. The peak of oyster setting there is in July; spat will have grown to size sufficient to harbor one or more crabs by the peak of the crab invasions in September. Though invasive stages in oysters are found all winter, growth and development stop about the first of November when water temperatures begin to drop below 15° C. Surprisingly small spat may be invaded. Two crabs were found in an oyster 4.2 mm. long, and in larger spat up to seven crabs were found in a single specimen. The crabs prefer to invade spat or yearling oysters rather than older ones (76.7, 54.6, and 21.5, being respective infestation percentages for a given year class of crabs), but survival rate of crabs is better in yearlings and older oysters.

Following the invasive stage are two ill-defined stages designated as prehard. These stages, described by Christensen and McDermott (1958), are soft and resemble later posthard stages of the females (carapace width: male, 1.4–4.6; female, 0.75–2.7 mm.). The legs are rounded and not adapted for swimming. These stages are found in all parts of the water-conducting system of infested oysters. In the region of Delaware Bay, most young crabs reach the prehard stages before growth ceases in fall and they overwinter in these stages. Development resumes when temperatures rise above 15° C.

The hard stage, formerly regarded as the invasive stage, is characterized above. On the average, males are larger than females, as they are in the preceding stages. The form of this stage resembles that of the invasive stage, and males of this stage swim freely. This is the copulatory stage, and the males normally die in this stage.

The succeeding female stages, described by Stauber (1945), resemble the adult female, and are found only in the host on the gills. Stage II (the hard stage was designated as stage I by Stauber) has a thin flexible carapace but a narrow abdomen contained wholly in the sternal groove (carapace width, 1.3–3.1 mm.). Stage III has an abdomen extending beyond the depression in the sternum (carapace width, 2.6–4.4 mm.). Stage IV

has a relatively wide abdomen reaching the coxae of the legs in most cases (carapace width, 3.6–8.9 mm.). Stage V is the adult female described above.

The posthard stages are passed through rapidly. In Delaware Bay by mid-July, 62 percent of females have developed from the overwintering stage to maturity. By mid-August, 95 percent are mature and more than half are ovigerous; thus, *P. ostreum* reaches maturity within its first year. Males live 1 year or less, but females continue to grow after they have hatched their first batch of eggs and may live to an age of 2 or 3 years, though many probably die after they have hatched their eggs in the second summer. In the second or third year, females may become ovigerous as early as mid-June, and ovigerous yearlings may occur as late as mid-October. Farther south the breeding season is more extended, and ovigerous females have been collected near Ocracoke, N.C., as early as mid-April.

Ovigerous females measuring 9.4 and 10.8 mm. in width carried 7,957 and 9,456 eggs respectively. It is not known how long a female carries eggs, but it is believed to be 3 to 5 weeks. The females produce only one batch of eggs the first year but in a second or third year may produce twice.

Except for the brief free-swimming periods in the invasive hard stages, the crabs lead a parasitic existence. Stauber (1945) and Christensen and McDermott (1958) both found that the crab feeds on food filtered from water by the host by picking food strings from the margins of the gills with its chelipeds. The crab also will catch newly formed mucus-food masses with its walking legs and then reach beneath the abdomen with its chelipeds, comb the legs, and pass the food on to the mouth. The method of feeding for young crabs not on the gills is unknown, but they may filter food with the mouth parts. Posthard stages are found only on the gills, indicating that feeding on the food-laden mucus alone can insure adequate food for rapid growth and egg production. Growth of females is positively correlated with size of host and is probably related to food supply and amount of water pumping by the host.

The ordinary feeding activities are harmful to the host (Stauber, 1945), particularly causing gill erosion of two types, local erosion of one or more lamellae, and an extensive shortening of demibranchs from the anterior end of gills to a point ventral to the adductor muscle. Christensen and McDermott (1958) noted that this erosion is a progressive process and nearly all infested oysters show some gill damage, some few older oysters having hardly any gill tissue left. Usually, however, only presence of a mature crab over a long time will noticeably affect growth of an oyster in normal environmental circumstances.

Pinnotheres maculatus Say. Mussel crab

Figure 190

Pinnotheres maculatum Say, 1818, p. 450.

Pinnotheres maculatus: Rathbun, 1918b, p. 74, text-figs. 35–36, pl. 17, figs. 3–6 (rev.).—Hay and Shore, 1918, p. 443, pl. 35, fig. 10.

Recognition characters.—Mature female: carapace suborbicular, somewhat broader than long, thick and firm but not hard, convex, smooth; surface uneven, covered with a short, dense, deciduous tomentum. Gastrocardiac area higher than, and separated by depressions from, branchiohepatic area. Front slightly advanced, approximately one-fifth width of carapace, subtruncate in dorsal view, slightly bilobed. Orbits small, subcircular, eyes spherical. Antenna longer than width of orbit; antennule large, obliquely transverse. Buccal mass roughly quadrangular, crescentic, much broader than long; ischium and merus of external maxilliped united; propodus larger than carpus; dactyl narrow, curved, spatulate, attached near middle of propodus, and reaching to near extremity of propodus.

Chelipeds moderately stout, articles subcylindrical and more or less pubescent; carpus elongate; palm thick, blunt edged, increasing in size distally; fingers stout, fitting closely together with tips hooking past each other; immovable finger nearly horizontal; dactyl with tooth near base fitting into sinus with tooth at either side on immovable finger. Walking legs slender, hairy above and below; second pair longest, shorter than chelipeds; first three dactyls falcate, shorter than propodi; last leg shortest, turned forward and upward, with long dactyl equaling propodus.

Abdomen large, extending to bases of legs.

Measurements.—Carapace: length, 13.7 mm.; width, 14.3 mm.

Color.—Obscure brown.

Recognition characters.—Mature male: Carapace flat, subcircular, diameter about half as great

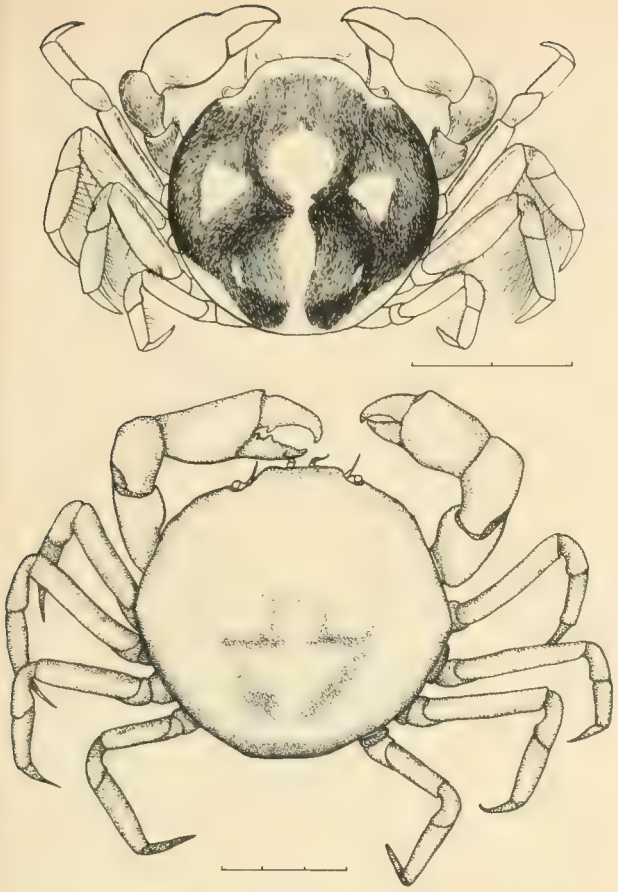

FIGURE 190.—*Pinnotheres maculatus* Say. Upper drawing: male in dorsal view, 2 mm. indicated; Lower drawing: female in dorsal view, 3 mm. indicated.

as female, somewhat longer than wide, harder than female. Regions superficially defined more by color than by structural prominence, light areas mostly elevated, usually allowing pubescence to wear; gastric, cardiac, and branchial regions separated by broad, shallow, confluent indentations. Front broad, prominent, depressed, slightly bilobed, approximately one-third width of carapace. Orbits subcircular, eyes large. Antennae somewhat longer than width of orbit.

Chelipeds shorter than in female, hands stouter. Walking legs wider, especially propodal articles of first three legs; posterior surface overlaid with thin fringe of hairs attached near upper margin; last leg relatively shorter than in female, not reaching propodus of third, dactyl more nearly like third than in female.

Abdomen at middle approximately one-third width of sternum, gradually narrowing from third to seventh segment, sides of third convex, of seventh obtusely rounded; sutures between segments of abdomen and sternum with narrow lines of dark pubescence.

Measurements.—Carapace: length, 9.1 mm.; width, 8.7 mm.

Color.—Striking light dorsal color pattern of bare spots on a background of dark pubescence consisting of a median stripe constricted in middle and behind, a subtriangular spot on each side in front of middle, and a linear spot on each side behind. Chelipeds with dark pubescence on inner and upper surface of carpus, a bit on upper surface of merus and inner side of palm proximally, otherwise scattered flecks on hands and walking legs.

Variations.—Young females resemble dark-colored males except in shape of the abdomen and the character of its appendages. Such females are free swimming and range upward in length to 5.2 mm. More mature females, light colored and commensal or parasitic in habit, range from 3.3 mm. in length upward. In such small and medium sized females the long hair on the legs persists.

Some males resemble mature females in coloration and structure of legs, ranging in length from about 4 mm. upward. Such males are commensal or parasitic in habit.

Individuals vary in stoutness of chelae, and in length and curvature of dactyls on the second legs. Normally this dactyl is like the dactyls on the first and third legs, but may be straightened and longer, and may occur on one or both sides of an individual and in different individuals in the same lot.

Habitat.—Mature males and females are commensal or parasitic in *Mytilus edulis*, *Modiolus modiolus*, *M. americanus*, *Mya arenaria*, *Aequipecten gibbus*, *A. irradians*, *Placopecten magellanicus*, oyster (?), *Atrina serrata*, and in tubes of *Chaetopterus variopedatus*, from *Molgula robusta*, the pharynx of *Bostrichobranchus pilularis*, and on *Asterias vulgaris*. The free-swimming stages have been found in bays and sounds. Surface to 25 fathoms.

Type locality.—Given as—"inhabits the muricated *Pinna* of our coast."

Known range.—Off Marthas Vineyard, Mass., to Mar del Plata, Argentina.

Remarks.—Though no detailed life-history studies have been made on this species comparable

to those on *P. ostreum*, more incidental data are available on mature individuals of both sexes from casual collecting. Ovigerous females have been found through most of the range of distribution. They have been reported in January from St. Thomas, March from Jamaica, May to November from Florida, June to January from North Carolina, July to September from Massachusetts and Rhode Island, and in June in Brazil (Rathbun, 1918b, and U.S. National Museum records). Hyman (1924a) described the first stage zoea which, unlike the zoeae of *P. ostreum*, has well-developed spines on the carapace. These zoeae are common near Beaufort, N.C., throughout the summer.

As in *P. ostreum*, the hard stage is found in both males and females and, though both swim actively, the males predominate in open water. An invasive stage may precede the relatively large hard stage as in *P. ostreum*. Unlike *P. ostreum* males, at least some *P. maculatus* males apparently live beyond the hard stage, for larger, somewhat globose males, resembling females in adaptation to parasitic or commensal life, occur in some hosts (see variations above).

Welsh (1932) found the swimming velocity of *P. maculatus* larvae to be greatly influenced by temperature and light intensity. The larvae are sensitive to only a small range of light intensity. At temperatures between 20° and 25° C. the maximum velocity of swimming is attained at intensities between 10 and 25 meter-candles. When series of measurements are made to determine the effective light at different constant temperatures, it is found that, besides a marked effect on general activity, there is a change in the relationship of velocity to intensity; slopes of curves showing these relationships change, and the maximum possible velocity of swimming for each temperature is reached earlier at the higher temperatures.

Genus ***Parapinnixa*** Holmes, 1894

Rathbun, 1918b, p. 107.

Parapinnixa bouvieri Rathbun

Figure 191

Parapinnixa bouvieri Rathbun, 1918b, p. 111, text-fig. 60, pl. 25, figs. 4–10.

Recognition characters. — Minute. Carapace smooth, shining, not more than twice as wide as long, longitudinally very convex, slightly convex transversely, sides arcuate; widest part with a thin pubescent margin on lower edge; anterior margin nearly straight, a row of four distant pits behind margin. Frontoorbital width about one-third carapace width. Front broadly triangular, deflexed, tip invisible in dorsal view, edge emarginate and pubescent; a pubescent groove running parallel to and immediately behind front terminating in orbital margins. Orbits circular, filled by eyes, cornea black, visible from above. Antennular cavities large, not wholly separated from each other or from orbits, and extending laterally beyond minute antennae. Outer maxilliped triangular when folded in place, two free corners rounded, longitudinal side approximately two-thirds as long as posterior side; ischium and merus fused, obliquely truncate distally leaving first joint of palp exposed; propodus elongate, distally tapering; dactyl small, suboval, both articles folding under merus.

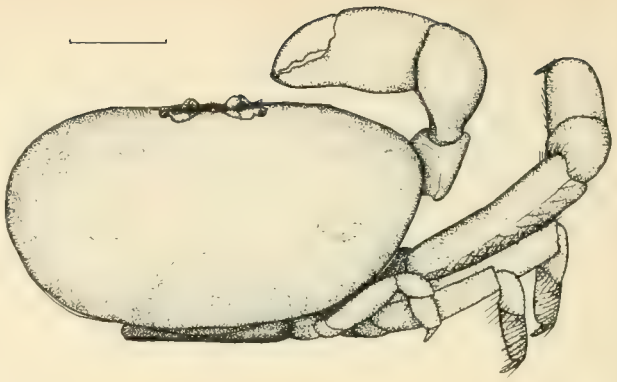

FIGURE 191.—*Parapinnixa bouvieri* Rathbun. Ovigerous female in dorsal view, legs of left side not shown, 1 mm. indicated.

Chelipeds short, stout, merus especially, partly hairy inside; palms thick, hairy outside; lower margin convex; immovable finger subtriangular, broad at base, a small tooth on gripping edge near tip; dactyl with small basal tooth, remainder of edge finely and irregularly denticulate. Walking legs with edges more or less pubescent, second and third pairs with line of long hairs applied to posterior surface of carpus and propodus; first leg thick, merus not reaching laterally beyond carpus of cheliped; second and third leg about equal; fourth small, not exceeding merus of third; dactyls of second and third legs longer and more slender than of first and fourth.

Male abdomen with sides gradually convergent, seventh segment not more than 1.5 times as long as wide; female abdomen with sides of triangular portion straight.

Measurements.—Carapace: female, length, 1.6 mm., width, 3.1 mm.; male, length, 2 mm., width, 3.5 mm.

Habitat.—Approximately 3 or 4 to 40 fathoms.

Type locality.—Off Cape Catoche, Yucatan, [Mexico]; *Albatross* station 2362.

Known range.—Off Charleston, S.C.; south of Tortugas, Fla.; Puerto Rico; and type locality.

Remarks.—Ovigerous females have been taken in Florida in August. The ovigerous specimen taken in Puerto Rico (no date) was found among ventral spines of a rose sea urchin (J. A. Rivero, U.S. National Museum).

Genus ***Dissodactylus*** Smith, 1870

Rathbun, 1918b, p. 114.—Hemming, 1958b, p. 31.

Dissodactylus mellitae Rathbun

Figure 192

Echinophilis mellitae Rathbun, 1900a, p. 590.
Dissodactylus mellitae: Rathbun, 1918b, p. 117, text-fig. 66, pl. 28, figs. 7–8 (rev.).—Hay and Shore, 1918, p. 444, pl. 36, fig. 1.

Recognition characters.—Minute. Carapace about one-fourth wider than long, slightly wider at lateral angles than posteriorly, dorsal surface convex, smooth, and polished except anterior portions slightly pubescent. Edge of front concave, fringed with short hairs. Anterolateral borders arcuate, with a fine raised rim curving inward on carapace at lateral angles and continuing mediposteriorly for some distance; posterior margin sinuous. Orbits opening medially, eyes small.

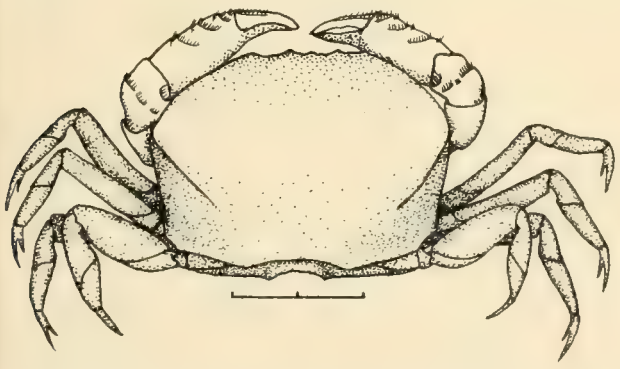

FIGURE 192.—*Dissodactylus mellitae* Rathbun. Animal in dorsal view, 2 mm. indicated.

Outer maxilliped with fused, spatulate merus and ischium; outer edge of carpus arcuate; propodus quadrate.

Chelipeds short and stout; hand longer than other articles combined, cylindrical, upper and outer faces bearing a few impressed, short, oblique lines with short appressed hairs extending distally; fingers considerably shorter than palm, bent inward and curved, opposable margins with tufts of short bristles; carpus with a distal fringe of short hairs and an impressed line similar to those on chelae; merus short and stout, lower surface with oblique lines. First, second, and third walking legs stout, margins fringed with short hairs, dactyls deeply bifid; fourth walking legs with styliform dactyls, fringed with long hairs on margins.

Abdomen of male with first and second, and third to fifth segments partially fused, margins convex; telson subtriangular with convex sides. Abdomen of female with first segment linear, second to fourth fused; telson broadly triangular, half as wide as sixth segment, sides sinuous.

Measurements.—Carapace: male, length, 2.9 mm., width, 3.5 mm.; ovigerous female, length, 3.3 mm., width, 4.5 mm.

Color.—Light, with scanty dark mottlings which persist in alcohol and are then of purplish color (Rathbun, 1918b).

Habitat.—This species clings to the outside of the keyhole urchin *Mellita quinquesperforata* and the sand dollars *Echinarachnius parma* and *Encope michelini.* The crabs are easily overlooked because as the sand dollars are lifted from the water, the small crabs may move about and drop off. Shallow water to 11.5 fathoms.

Type locality.—Pensacola, Fla., on *Mellita quinquesperforata.*

Known range.—Western part of Vineyard Sound, Mass., to Charleston, S.C.; western Florida.

Remarks.—Hyman (1924a) described the first zoeal stage of this crab, comparing it to the zoea of *Pinnotheres maculatus*, and reported it as common in plankton tows in the Beaufort, N.C., area in summer. Ovigerous females occur there during the same period, and are reported from Narragansett Bay in August (Rathbun, 1918b), and in Florida from July to October (Wass, 1955, in part).

Subfamily **Pinnothereliinae**

Carapace transverse, usually broadly so. Ischium of external maxilliped usually distinct from merus, though smaller and sometimes imperfectly united with it. Merus longitudinal or somewhat oblique; palp of good size, sometimes as large as merus-ischium (Rathbun, 1918b).

Genus ***Pinnixa*** White, 1846

Rathbun, 1918b, p. 128.—Hemming, 1958b, p. 35.

KEY TO SPECIES IN THE CAROLINAS

a. Posterior part of carapace with conspicuous, sharp, transverse ridge extending uninterruptedly from side to side_____*cristata* (p. 210).
aa. Posterior part of carapace without ridge, or with ridge on cardiac region only.
  b. Chela with immovable finger bent downward.
    c. Propodus of third walking leg less than twice as long as wide_____*chactopterana* (p. 210).
    cc. Propodus of third walking leg slender, twice or more than twice as long as wide___*sayana* (p. 212).
  bb. Chela with immovable finger straight or nearly so, not bent downward.
    c. No cardiac ridge present_____*retinens* (p. 212).
    cc. With cardiac ridge present.
      d. Merus of third walking leg with posterior surface not deeply cupped out____*cylindrica* (p. 213).
      dd. Merus of third walking leg with posterior surface deeply cupped out_____*lunzi* (p. 214).

Pinnixa cristata Rathbun

Figure 193

Pinnixa cristata Rathbun, 1900a, p. 589.—1918b, p. 134, text-fig. 78, pl. 29, figs. 8–9 (rev.).—Hay and Shore, 1918, p. 446, pl. 36, fig. 5.

Recognition characters.—Carapace short, surface punctate, wrinkled, and microscopically granulate, slightly pubescent at extreme outer corners; a high, sharp, almost straight ridge extending without a break entirely across carapace somewhat in front of posterior border; a deep furrow behind gastric region. Anterolateral margin with a raised crest stopping short of hepatic region; posterior margin wide, concave. Front deflexed, not advanced. Orbit no wider than half of front.

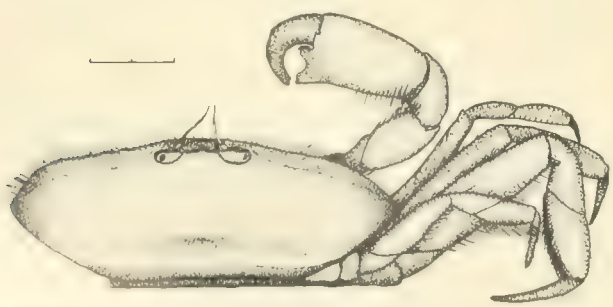

Figure 193.—*Pinnixa cristata* Rathbun. Male in dorsal view; legs of left side not shown, 2 mm. indicated.

Chelipeds rather stout; palm oblong with upper and lower margins convex, surface covered with reticulate pattern of fine granulations; immovable finger short, deflexed, gripping edge with a truncate subbasal tooth, another small tooth distally forming a truncate tip; dactyl long, gaping, with inner margin bent in a curved right angle. Walking legs somewhat longer than in related species, sparsely hairy along margins only, third walking leg strongest; dactyls slender, slightly curved on first three, straight on last walking leg.

Measurements.—Carapace: female, length, 4 mm.; width, 11 mm.

Type locality.—Beaufort, N.C.

Known range.—Beaufort, N.C., to Edisto Island, S.C.; Grand Isle, La., to Long Lake, Blackjack Peninsula, Aransas County, Tex. (Hedgpeth, 1950, and U.S. National Museum records).

Remarks.—The species has been taken from sandy beaches by digging or sifting in North Carolina and South Carolina, and Louisiana, and from the mouth of *Galeichthys felis* in Louisiana.

Pinnixa chaetopterana Stimpson

Figure 194

Pinnixa chaetopterana Stimpson, 1860a, p. 235.—Rathbun, 1918b, p. 151, text-figs. 93–94, pl. 33, figs. 3–6 (rev.).—Hay and Shore, 1918, p. 445, pl. 36, fig. 4.

Recognition characters.—Carapace transversely oval, somewhat more than twice as wide as long, more swollen in female than in male, surface uneven, sides densely pubescent. Regions well defined by pubescent grooves; cardiac region with an acute transverse crest broadly interrupted in middle forming two dentiform prominences, more conspicuous in male than in female; subbranchial region advanced, forming a prominent shoulder with granulated edge. Posterior margin concave. Front narrow, with a deep median groove.

Chelipeds stout, smooth, pubescent. Hand in male with distal palmar edge perpendicular; immovable finger short, deflected, truncate at tip, with a prominent rounded tooth on cutting edge; dactyl strongly curved, almost vertical, forming

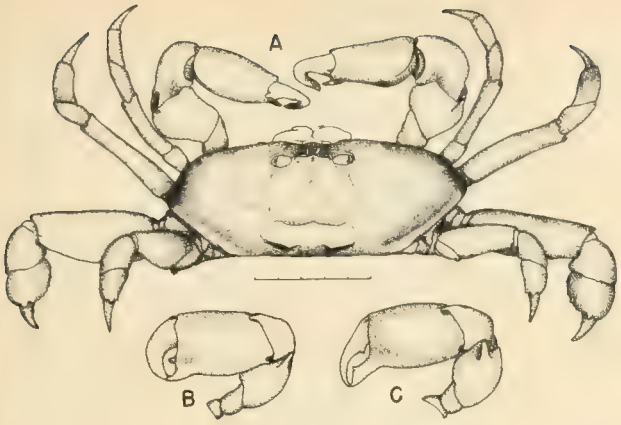

FIGURE 194.—*Pinnixa chaetopterana* Stimpson. A, male in dorsal view; B, chela of male in frontal view; C, chela of female in frontal view; 5 mm. indicated.

oval gape when closed with tips of fingers meeting. Hand of female relatively smaller; immovable finger with tooth somewhat beyond middle followed by an irregularly dentate, raised, cutting edge terminating in a blunt tip; dactyl with a small basal tooth, longer than in male, fingers agape proximal to cutting portion when closed with tips crossing each other. First and second pairs of walking legs slender, propodi with distal V-shaped row of spinules on lower border; dactyls with one or more short rows of spinules. Third pair longer and much stouter, conspicuously pubescent, and with inferoposterior margins of ischium, merus, and propodus dentate; fourth pair like third but smaller, with minute spinules on dactyls.

Male abdomen with sixth segment slightly constricted laterally at middle; telson semicircular.

Measurements.—Carapace: male, length, 6 mm., width, 14 mm.; female, length, 6 mm., width, 11 mm.

Variations.—Wass (1955) pointed out that two forms of this species occur on the northern Gulf of Mexico coast, a larger and smaller form.

Color.—Nearly white, but usually much obscured by brown or blackish hairs and by dirt collected in them; eggs bluish (various authors).

Habitat.—The large form of this crab lives commensally with the worms *Chaetopterus variopedatus* and *Amphitrite ornata*, and is seldom found outside their tubes. The small form lives in the upper portion of *Callianassa* burrows on the northern Gulf coast (Wass, 1955). Intertidal to 8.5 fathoms.

Type locality.—Charleston Harbor, S.C., on muddy or clayey shores in tubes of *Chaetopterus variopedatus* [=*pergamentaceus*].

Known range.—Wellfleet, Mass., to South Carolina; Punta Rassa, Fla., to Galveston, Tex.; Rio de Janeiro, and Villa Bella, São Sebastião, Brazil.

Remarks.—Ovigerous females have been reported from Beaufort, N.C., between April (Gray, 1961) and late October (Enders, 1905), from Florida in October (Wass, 1955) and February (Gray, 1961), and from southern Massachusetts in July and August (Pearse, 1913; Rathbun, 1918b). Otherwise they are known from South Carolina in February. Faxon (1879) and Hyman (1924a) described the first zoeal stage.

Some habits of this crab were observed by Pearse (1913) at Woods Hole, Mass. The species is strongly thigmotactic. Crabs placed on sand in an aquarium usually buried themselves, but soon explored the surface and entered and remained in glass tubes left lying on the sand. In experiments, crabs found a buried, artificial "*Chaetopterus* tube" by accident. Adult crabs could enter or leave this tube. The crabs moved either forward or sideways on sand. The third walking leg was the chief locomotor organ, but in tubes the crabs braced themselves with all the legs.

Crabs placed in standing water in an artificial worm tube were able to exist for 8 days before leaving the tube for better aerated water. The crabs' respiratory currents were feeble and inconstant in direction and force. Crabs were usually fouled with encrusting organisms and they took no trouble to clean their bodies except for mouth parts, eyes, and antennae. They fed by extending the fringed external maxillipeds and sweeping them toward the mouth, filtering small particles from the water, then cleaning the fringe with other mouth parts.

Gray (1961, see also account for *Polyonyx gibbesi*) described *Pinnixa chaetopterana* as primarily a mud crab and a facultative commensal of *Chaetopterus*. He found that the crabs readily enter and leave the tubes of the host, and if diameter of the parchment chimney of the worm tube is too small, the crab bites a hole at the base of the chimney to make an entrance or exit.

Pinnixa sayana Stimpson

Figure 195

Pinnixa sayana Stimpson, 1860a, p. 236; Rathbun, 1918b, p. 156, text-fig. 98, pl. 34, figs. 2–4 (rev.).—Hay and Shore, 1918, p. 446, pl. 36, fig. 3.

Recognition characters.—Carapace smooth, polished, lightly pubescent on sides, depressed at middle, a low, ill-defined, transverse ridge parallel with and close to posterior margin extending about one-third width of carapace. Anterolateral slope with similar ridge, lateral two-thirds of crest beaded. Front deeply grooved above.

Chelipeds with hands stout, compressed, hardly twice as long as broad; immovable finger very short, with truncate basal tooth; dactyl strongly curved. Walking legs long and slender, smooth; first walking leg reaching to propodus of second; second and third leg same length; fourth reaching beyond middle of carpus of third; merus of third leg approximately 3.5 times as long as wide, lower margin, and that of propodus, minutely denticulate; dactyls of first two legs slightly curved, of third straight, posterior edge of last dactyl slightly convex.

Measurements.—Carapace: male, length, 5 mm., width, 10 mm.; female, length, 4 mm., width, 7 mm.

Variations.—Females differ from males in that the cardiac ridge is lower and less sharp, the fingers do not gape, the immovable finger is longer and less bent, and the dactyl on the chela is more oblique.

Color.—Almost white, but lightly stained with brown.

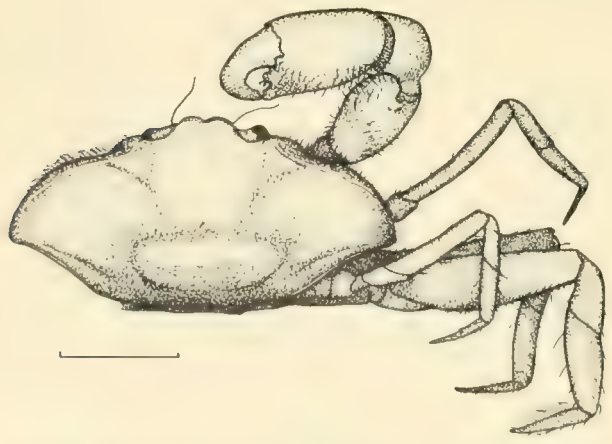

FIGURE 195.—*Pinnixa sayana* Stimpson. Male in dorsal view, legs of left side not shown, 1 mm. indicated.

Habitat.—The species has been found free in the water, has been dug out of mud, and is said to be found in the tubes of *Arenicola cristata;* shore to 26 fathoms.

Type locality.—Mouth of Beaufort Harbor, N.C., 6 fathoms, sandy mud.

Known range.—Vineyard Sound, Mass., to Beaufort, N.C.; Sarasota Bay, Fla., to Grand Isle, La.

Remarks.—Ovigerous females have been reported in August from Narragansett Bay, R.I. (Rathbun, 1918b), and are known in September from Louisiana. The last zoeal stage of a *Pinnixa*, commonly found off the New England coast and described by Faxon (1879), was tentatively referred to this species by Smith (1880a). Both Faxon and Smith found the first crab stage to follow immediately the last zoeal stage. These stages in development of *P. sayana* were summarized and illustrated by Hyman (1924a).

Pinnixa retinens Rathbun

Figure 196

Pinnixa retinens Rathbun, 1918b, p. 139, text-figs. 83–84, pl. 41, figs. 1–2.

Recognition characters.—Carapace nearly twice as wide as long, almost flat, except sloping downward toward margins; regions indicated. Lateral margin marked by sharp, granulate ridge reaching to subhepatic sulcus, no cardiac ridge; posterior margin preceded by a subparallel groove. Outer maxilliped with obliquely spatuliform dactyl attached to middle of inner margin of propodus.

Chelipeds small, approximately as long as first leg; hand with lower margin straight, suboblong, marginate below; fingers slender, subequal, not gaping; dactyl with tooth at proximal third of gripping edge. First and second walking legs similar; second a little longer, dactyls slightly curved, long, pointed. Third walking leg stout, exceeding second by length of dactyl and half of propodus; lower edge of ischium, merus, and propodus armed with stout spinules; posterodistal end of ischium prolonged in a stout, curved spine with point directed upward and backward; dactyl more curved than in first and second legs, pointed. Last leg extending to distal end of third merus; dactyl stout, nearly straight, tip curved slightly upward.

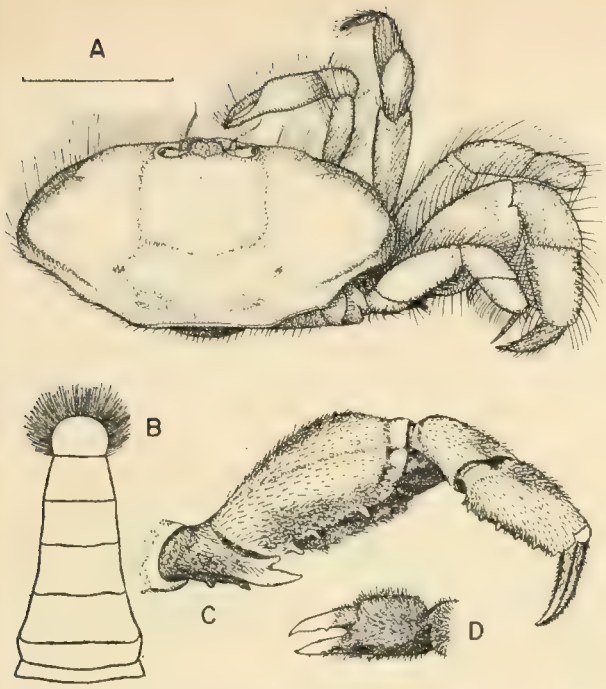

FIGURE 196.—*Pinnixa retinens* Rathbun. A, female in dorsal view, legs of left side not shown, 5 mm. indicated; B, male abdomen; C, male third walking leg, lower side; D, male left chela; B–D, holotype approximately × 9 (after Rathbun, 1918b).

Abdomen constricted at base of second segment, widest between second and third, and tapering to base of telson; telson wider than long; anterior and posterior margins of sternal segments granulate.

Measurements.—Carapace: male, length, 4 mm., width, 7 mm.; ovigerous female, length, 6 mm., width, 12 mm.

Habitat.—An ovigerous female was taken from the burrow of *Upogebia affinis* at Alligator Harbor, Fla., in June (Wass, 1955). Small specimens have recently been taken from mud bottom in Chesapeake Bay (Wass, personal communication). Near low-tide mark to 20 fathoms.

Type locality.—Chesapeake Bay, off Poplar Island, Md., 20 fathoms, soft bottom.

Known range.—Chesapeake Bay; Alligator Harbor, Fla.; Aransas area of Texas coast (U.S. National Museum records).

Remarks.—Though this species has never been reported in the Carolinas, its occurrence in the above localities would indicate that it probably ranges at least between them.

Pinnixa cylindrica (Say)

Figure 197

Pinnotheres cylindricum Say, 1818, p. 452.

Pinnixa cylindrica: Rathbun, 1918b, p. 159, text-fig. 99, pl. 35, figs. 5, 8 (rev.).—Hay and Shore, 1918, p. 446, pl. 36, fig. 2.

Recognition characters.—Carapace smooth, polished, punctate, punctations small and scarce in middle third, large and more numerous elsewhere; pubescent at extreme outer corners; depressed in middle; anterior cardiac region separated from gastric and branchial regions by a groove. Anterolateral portions with a sharp granulate crest not reaching cervical suture; middle of cardiac region crossed by a transverse (sometimes inconspicuous) ridge; posterior border short, somewhat concave. Front not prominent, bilobed, with submarginal groove.

Chelipeds moderately stout, smooth, punctate; hands suboval, approximately 1.5 times as long as wide; fingers horizontal, subequal in length, tips strongly hooked, overlapping when closed, leaving a gape; immovable finger with tooth near tip; dactyl with a tooth near middle; a finely milled crest running from tip of immovable finger backward and upward approximately two-fifths length of palm on outer surface. First walking leg slender, reaching to propodus of second; second stouter, reaching to middle of dactyl of third; third leg stoutest, merus 1.6 times as long as wide, distally narrowed, upper and lower margins finely granulate; fourth short; dactyls nearly straight, that of fourth leg convex posteriorly, slightly concave anteriorly.

Abdomen of male with sixth segment constricted laterally, constriction narrower than telson.

Measurements.—Carapace: male, length, 7 mm., width, 14 mm.; female, length, 10 mm., width, 20 mm. (McDermott, 1962).

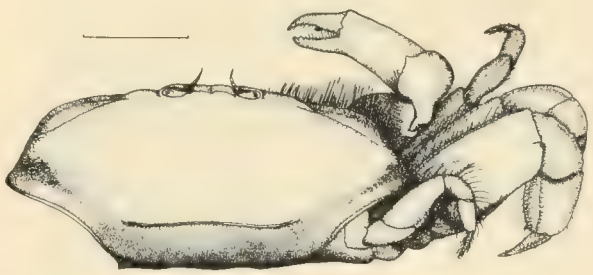

FIGURE 197.—*Pinnixa cylindrica* (Say). Female in dorsal view, legs of left side not shown, 5 mm. indicated.

763-049 O—65——15

Color.—Yellowish gray, light to dark brown, or sometimes grayish, and mottled with dark gray and/or white. Rhythmic chromatophore changes as well as genetic differences may control observed variations (McDermott, 1962).

Habitat.—The species lives in burrows of *Arenicola cristata* Stimpson (Wass, 1955; McDermott, 1962), and possibly with other large annelids; shallow water to 20 fathoms.

Type locality.—Jekyll Island, Ga.

Known range.—North Falmouth, Mass., to Alligator Harbor, Fla.

Remarks.—McDermott (1962) summarized existing knowledge of the habits of this species and added numerous ecological observations. He reported the crab for the first time from New Jersey, finding it associated with 76 percent of the lugworms collected during summer. Crabs and worms were collected by manual digging. With one exception, single crabs were found on worms.

Of 18 female crabs found in July, 16 were ovigerous. One captive female produced eggs on July 7 and liberated zoeae "around" August 5. Crabs which liberated zoeae when collected produced new sponges of eggs which were in late stages of development approximately 30 days later. McDermott judged that this species produces at least two egg masses in a breeding season. Molting between broods did not occur in the laboratory.

Associates of *P. cylindrica* were found to be *Zoothamnium sp.*, attached *Crepidula convexa* Say, and colonies of *Triticella elongata* (Osburn).

Pinnixa lunzi Glassell

Figures 198–199

Pinnixa lunzi Glassell, 1937, p. 3, figs. 1–8.

Recognition characters.—Carapace slightly more than twice as wide as long, punctate, regions indicated, borders flanged, with a shoulder formed near wide lateral angle. Gastric and cardiac regions separated by a depression connecting with a deeper depression on each side of these regions; a prominent cardiac ridge extending transversely almost across carapace with an abrupt slope from crest of ridge to posterior border. Front prominent, bilobed, truncate, upturned over antennules.

Chelipeds stout; hands of male shorter and stouter than in female, appearing disproportionately small in female; palm with margins subparallel in female, widest at base of dactyl in male; in both sexes fingers gaping; immovable finger horizontal, armed with row of small teeth, distal tooth largest; dactyl stout, curved, armed with median lobe. Walking legs stout. First two lightly crested with setae on merus; carpus crested with a sharp beaded rim; propodus armed with a row of fine, sharp, brown spinules; dactyls contorted, sharp pointed, fluted, with rows of small,

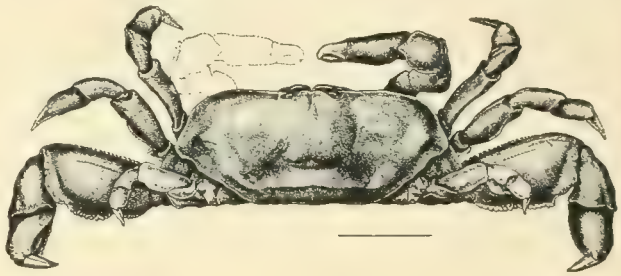

FIGURE 198.—*Pinnixa lunzi* Glassell. Male holotype in dorsal view, 7 mm. indicated (after Glassell, 1937).

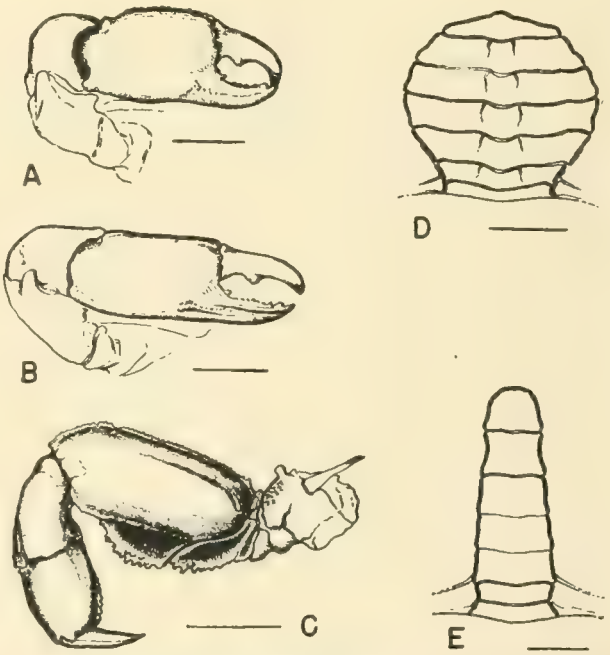

FIGURE 199.—*Pinnixa lunzi* Glassell. A, right chela of male; B, right chela of female, 3 mm. indicated; C, left third walking leg of female, 4 mm. indicated; D, abdomen of female, 6 mm. indicated; E, abdomen of male, 3 mm. indicated (after Glassell, 1937).

sharp, forward pointing spinules on crests. Third leg large; merus with two separated, upper, crenulated margins, lower border tuberculate, posterior surface with a deep, pubescent concavity, smooth within; ischium at lower distal end extending well past base of merus and with meral concavity continued on posterior face, lower border tuberculate; carpus and propodus together equal in length to upper length of merus; dactyl stout, nearly straight, without minute spinules. Fourth leg similar to third but smaller, merus with lower border tuberculate, dactyl slightly upturned at tip.

Male abdomen with telson semioval, sides not wider than concave sided sixth segment; third, fourth, and fifth segments partially fused.

Measurements.—Carapace: male, length, 9 mm., width, 21 mm.; female, length, 9 mm., width, 21 mm.

Color.—In alcohol, a muddy bluish brown; legs, abdomen, and chelipeds ivory.

Type locality.—Isle of Palms (about 15 miles northeast of Charleston, S.C.), washed on beach, under drift material.

Remarks.—The above account is taken chiefly from Glassell (1937). The types are the only known specimens and the host and habitat are unknown.

Family **Palicidae**

Carapace broadly transverse, subquadrilateral. Anterolateral margins dentate. Frontoorbital width great, front dentate. Orbits and eyes large. Buccal cavity quadrate, outer maxillipeds not covering it; ischium of third maxillipeds strongly produced forward on inner side; merus small, subtriangular, with a notch on inner distal side for articulation of palp. Afferent channels to branchiae opening at bases of chelipeds; efferent channels at anteroexternal angles of buccal cavity.

Chelipeds of moderate size, often unequal in male, usually tuberculate or granulate. Next three pairs of legs long, slender, and rough; last pair either very short and slender, subdorsal, smooth, or similar in position and ornamentation to other legs, and near size of first walking leg. Abdomen of male much narrower than sternum (Rathbun, 1918b).

Genus ***Palicus*** Phillipi, 1838

Rathbun, 1918b, p. 183; Holthuis and Gottlieb, 1958, p. 104.

KEY TO SPECIES IN THE CAROLINAS

a. Merus of second and third walking legs with an obtuse lobe at superodistal angle; frontal notch shallow, forming nearly a right angle at base_____*alternatus* (p. 215).

aa. Merus of second and third walking legs with a prominent, sharp pointed lobe at superodistal angle; frontal notch deeper than wide_____*faxoni* (p. 216).

Palicus alternatus Rathbun

Figure 200

Palicus alternatus Rathbun, 1897a, p. 95.

Cymopolia alternata: Rathbun, 1918b, p. 188, text-fig. 117, pls. 42–43 (rev.).

Recognition characters.—Carapace broader than long, somewhat depressed, elevations covered with small tubercles composed of single or a few granules. Front broadly triangular, notched at middle, with four lobes or teeth, outer teeth less advanced than inner and broadly rounded. Eyes large; orbits deep, with upper border cut into teeth; middle tooth broad, obliquely truncate, bounded on each side by a V-shaped fissure; next tooth separated from outer tooth by a shallow sinus; outer tooth directed forward or a little outward, tip curved inward. First two anterolateral teeth dentiform with rounded tips, separated

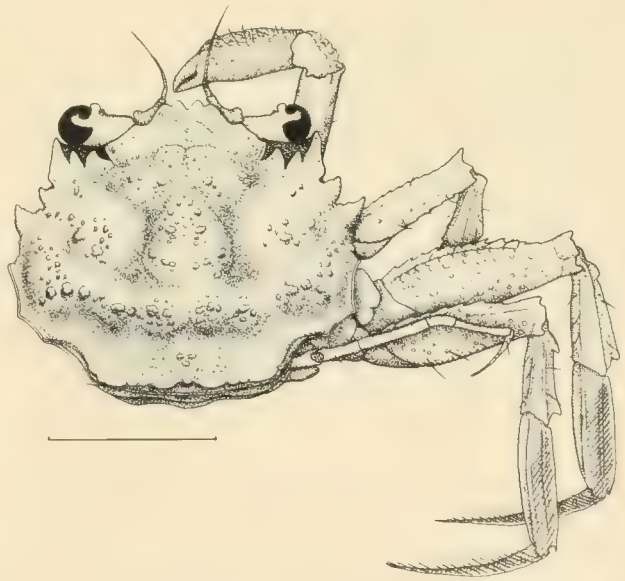

FIGURE 200.—*Palicus alternatus* Rathbun. Animal in dorsal view, legs of left side not shown, 5 mm. indicated.

by small V-shaped sinuses; third tooth rudimentary or in form of a small tubercle. Suborbital margin oblique, with two clefts; outer lobe nearly straight; inner lobe divided into two parts with inner angle produced in an acute tooth beyond triangular, pterygostomian lobe. Posterior margin bordered above by a thin, sinuous, elevated ridge broken into a variable number of unequal transverse tubercles with usually some granules interspersed.

Chelipeds of male occurring in two forms. In one form, chelipeds very unequal; on right side large and heavy, on left, slender and weak, both tuberculate and pubescent; carpus with an outer, laminated, lobed crest; hand surmounted by a similar double crest. Right hand very thick, width at distal end often equaling one-half length of carapace; immovable finger short, wide; dactyl strongly bent down, overlapping opposed finger and leaving a narrow gape. Left hand somewhat over one-third width of right, fingers long and narrow. In second, weaker form males, right hand about twice depth of left; fingers long and slender. Females with chelipeds more nearly equal.

Second pair of walking legs longer than others. First walking legs reaching middle of propodus of second, with posterior margin of propodus and proximal half of dactyl hairy in male; third walking leg reaching middle of dactyl of second, fourth leg slender, much shorter than third. Meri rough with squamous tubercles; with a single longitudinal groove on anterior surface, two on upper surface; first three meri with a superodistal lobe, subtriangular on first, subrectangular in second and third, lobe exceeding article in first, equal to article in second, not reaching end of article in third. Carpus with a rounded, anterior proximal lobe; anterior subdistal lobe low and rounded on first leg, triangular on second and third legs. Propodus with anterior margin convex, posterior margin straight.

Abdominal appendages of first form of male stout and twisted, tip bilobed, inner lobe thinner and longer than outer; second form of male with appendages weaker, not twisted, and tip less spreading.

Measurements.—Carapace: male, 7 mm., width, 8 mm.; female, length, 8 mm., width, 9 mm.

Variations.—This species shows great variation in structure. In some individuals the carapace is wider behind in proportion to its length than in typical individuals, and the sides are less parallel. There is no consistency in relative size of the anterolateral teeth, for in some the first are largest and all teeth point forward, but in others the second teeth are largest and point slightly outward. In some individuals the anterodistal tooth on the merus of the second and third legs is more produced than in typical specimens, and there is variation in the length-width proportions of the propodus of the second leg. Details of lobulation on the front and lower margin of the eye are also subject to variation.

Habitat.—The species has been taken from a variety of fine and coarse bottoms (Rathbun, 1918b); 4 to 60 fathoms.

Type locality.—Lat. 29°11′30″ N., long. 85°29′00″ W., 26 fathoms (south of Cape San Blas, Fla.).

Known range.—Cape Hatteras, N.C.; Gulf of Mexico along west coast of Florida from Cape San Blas to Key West.

Remarks.—Ovigerous females have been reported in Florida from January to August, and from North Carolina in October (Rathbun, 1918b, and U.S. National Museum records).

Palicus faxoni Rathbun

Figure 201

Palicus faxoni Rathbun, 1897a, p. 96.
Cymopolia faxoni: Rathbun, 1918b, p. 194, text-fig. 120, pl. 45, figs. 2–3 (rev.).

Recognition characters.—Carapace broader than long, sides converging anteriorly; adult female quite convex, surface hairy, and with numerous tubercles and granules. Front broadly triangular; four frontal lobes well marked, outer pair not much wider than inner, median emargination deeper than wide with end often rounded, lateral emarginations shallow. Eyes large; orbits deep, with upper border cut into teeth by V-shaped sinuses, middle and outer teeth triangular, subacute, middle one equilateral, outer one narrow and separated from outer orbital tooth by a shallower sinus; outer tooth directed forward, tip oblique, its lateral margin nearly straight. Lateral border with two similar, sharp-pointed teeth, second one smaller, outer borders convex, inner concave. Lower margin of orbit oblique, bilobed; inner lobe in advance of outer, divided in two, outer portion rounded, inner portion a small acute

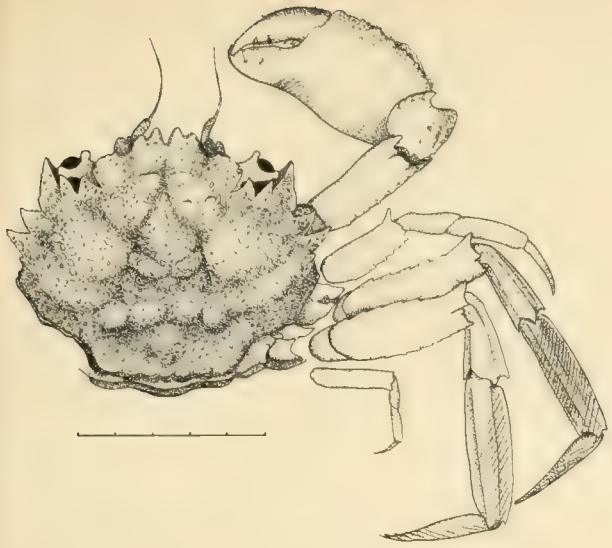

FIGURE 201.—*Palicus faxoni* (Rathbun). Male in dorsal view, legs of left side not shown; cheliped, second and third walking legs detached; first and fourth walking lags from female in Rathbun (1918b); 5 mm. indicated.

tooth somewhat obscured by ventrally bent pterygostomian lobe, sharp pointed at tip; outer lobe slightly convex. Posterior margin preceded by a tuberculate ridge.

Chelipeds in both sexes somewhat unequal, right hand approximately twice as wide as left. Walking legs short and broad; first three meral articles with a large, flat, acute distal spine, posterior distal tooth of merus sharp; carpal lobes prominent, distal one of second and third legs acute; propodus of second and third legs widening distally, dactyls wide, posterior margin sinuous.

Measurements.—Carapace: male, length, 10 mm., width, 10 mm.; female, length, 10 mm., width, 11 mm.

Habitat.—Thirty-two to 51 fathoms.

Type locality.—Off Cape Hatteras, N.C., 49 fathoms.

Known range.—Type locality; off Jacksonville, Fla.; off Yucatan, Mexico; off Cabo Frio, Rio de Janeiro, Brazil(?).

Family **Grapsidae**

Front quite wide; carapace usually quadrilateral, with lateral borders either straight or slightly arched, and orbits at or near anterolateral angles. Buccal cavern square; generally a gap, often large and rhomboidal, between external maxillipeds. Male openings sternal. Palp of external maxillipeds articulating either at anteroexternal angle or at middle of anterior border of merus, exognath either slender or broad. Interantennular septum broad. Division of orbit into two fossae accented (Rathbun, 1918b).

KEY TO SUBFAMILIES, GENERA, AND SOME SPECIES IN THE CAROLINAS

a. Antennules folding beneath front of carapace in usual way.
  b. Third maxillipeds without a pubescent oblique ridge.
    c. Lower border of orbit running downward toward buccal cavern (Subfamily Grapsinae).
      d. Carapace decidedly broader than long. *Pachygrapsus transversus* (p. 217).
      dd. Carapace about as long as broad; legs strongly fringed with hairs *Planes minutus* (p. 218).
    cc. Lower border of orbit not running downward toward buccal cavern, but supplemented by remote suborbital crest in line with anterior border of epistome (Subfamily Varuninae) *Euchirograpsus americanus* (p. 220).
  bb. Third maxillipeds with an oblique pubescent ridge crossing ischium and merus (Subfamily Sesarminae) *Sesarma* (p. 221).
aa. Antennules visible dorsally in deep clefts in front of carapace (Subfamily Plagusiinae).
  b. Carapace broader than long *Plagusia depressa* (p. 223).
  bb. Carapace longer than broad *Percnon gibbesi* (p. 224).

Subfamily **Grapsinae**

Front usually strongly deflexed. Lower border of orbit running downward toward buccal cavern. Antennal flagellum very short. External maxillipeds usually separated by a wide rhomboidal gap, not traversed by an oblique hairy crest; palp articulating at or near anteroexternal angle of merus; exognath narrow and exposed throughout. Male abdomen filling all space between last pair of legs (Rathbun, 1918b).

Genus ***Pachygrapsus*** Randall, 1840

Rathbun, 1918b, p. 240.

Pachygrapsus transversus (Gibbes). Mottled shore crab

Figure 202.

Grapsus transversus Gibbes, 1850, p. 181.
Pachygrapsus transversus: Rathbun, 1918b, p. 244, pl. 61, figs. 2–3 (rev.).—Hay and Shore, 1918, p. 447, pl. 36, fig. 9.

Recognition characters.—Small species. Carapace rectangular, about one-fourth broader than

FIGURE 202.—*Pachygrapsus transversus* (Gibbes). Animal in dorsal view, legs of left side not shown, 5 mm. indicated.

long, depressed, polished, with fine transverse plications, except oblique ones on branchial regions. Sides slightly arched, strongly converging posteriorly, and armed with a well-marked tooth behind orbital angle. Front slightly more than half as wide as carapace, edge sinuous and granulate, upper surface with four low elevations. Orbits oblique, approximately two-fifths width of front, lower border denticulate.

Chelipeds equal, much stouter than legs, 1.6 times longer than carapace in male, finely granulate; inner edge of merus produced in a laminate, toothed expansion; meri of all legs and carpus of cheliped transversely striated; carpus with blunt internal tooth; upper surface of palm with a marginal line, oblique striae on inner and lower side, an oblique line on outer surface near lower edge; fingers narrowly gaping except for large triangular tooth near middle of immovable finger. Merus of walking legs with posterodistal angle dentate; first and fourth walking legs subequal, second and third pairs longer and subequal, last three articles bristly and thorny. Female with conspicuous feathery hairs on carpus and propodus of first walking legs.

Male abdomen with telson broadly triangular.

Measurements.—Carapace: male, length, 11 mm.; width, 14 mm.

Color.—Variable; ground color almost black, olive green, yellowish, yellowish brown or dull gray, covered by irregular mottlings of dark brown, reddish or dark olive; usually darkest anteriorly with transverse ridges edged with greenish gray, reddish or dark brown; chelae often plain or reddish brown, tips light; walking legs brown or blackish with gray spots (various authors).

Habitat.—This species is found among rocks, on pilings, on roots of mangroves, and on sandy shores.

Type locality.—Key West, [Fla.].

Known range.—Cape Lookout, N.C., to Montevideo, Uruguay; Bermuda. Beyond this region the species has a wide distribution in tropical and subtropical seas and has been carried to higher latitudes than it normally inhabits by transport on ships' bottoms.

Remarks.—At Bermuda, where this crab is abundant, ovigerous females have been observed from April to July (Verrill, 1908). Ovigerous females have been reported from February to August in various parts of the Caribbean area (Rathbun, 1918b, in part), and are known from North Carolina in August and September. Lebour (1944) illustrated some of the larval stages of this species from their occurrence at Bermuda.

Pearse (1932b) reported the protozoan *Epistylis*, and Verrill (1908) the isopod *Leidya distorta* in the gill cavities of this crab.

In the past, occurrence of this crab in the Beaufort, N.C., area has been irregular and these intrusions from more southerly waters may reflect annual variations in temperature or occasional transport on vessels. As Verrill (1908) suggested, the range of this species may have been greatly extended by commerce in modern times.

Genus ***Planes*** Bowdich, 1825

Rathbun, 1918b, p. 253.—Chace, 1951.—Hemming, 1958b, p. 36.

Planes minutus (Linnaeus). Gulf weed crab; turtle crab; Columbus crab

Figure 203

Cancer minutus Linnaeus, 1758, p. 625.
Planes minutus: Hay and Shore, 1918, p. 448, pl. 36, fig. 6. Chace, 1951, p. 81, figs. 1a, 2 a, d, g, j, k, l, 3 a–h (rev.).—Holthuis, 1959, p. 240.

Recognition characters.—Carapace approximately as wide as long, subquadrate in young, trapezoidal in medium sized, laterally convex in old individuals, convex dorsally, smooth, but with faint oblique lines on outer part of branchial region. Front approximately half as wide as cara-

FIGURE 203.—*Planes minutus* (Linnaeus). Male in dorsal view, approximately × 2 (after Chace, 1951).

pace, decurved, usually slightly emarginate in middle, edges minutely denticulate or smooth. Eyes large; orbits large, lower margin granulate, tooth at inner angle equilateral, subacute, outer angle spiniform, behind it a small sinus.

Chelipeds large and heavy; merus and ischium with a thin serrate crest along inner margin terminating in two or three spines at distal end of merus; carpus with a strong blunt spine on inner face; hands inflated and smooth except for small sharp granules near lower margin; immovable finger bent downward, especially in males, dactyl curved, both with blunt teeth throughout length. Walking legs long, slender, and flattened; second and third legs subequal, fourth legs shortest; meri occasionally with an inconspicuous anterior subterminal tooth and a few posterior denticles; last three articles thorny and with a dense fringe of hair on anterior edge.

Abdomen of male rather broadly triangular; telson rather narrowly triangular, approximately as long as basal width.

Measurements.—Carapace: male, length, 19 mm., width, 19 mm. Length of a large series reported by Chace (1951), 3.7 to 19 mm.

Color.—Extremely variable; irregularly mottled or blotched with light greenish yellow or pale yellow on a darker olive-green ground color; or reddish-fawn color, more or less blotched with dark brown, and usually with a small white spot on each side or one large white spot on front of carapace (various authors).

Crozier (1918) observed no color change in a mahogany-colored *P. minutus* placed for a day on a lighter background. Hitchcock (1941) found three types of chromatophores in *P. minutus:* white, black, and yellow. The most prominent chromatophore is white. Color adaptation to different backgrounds is slow and though the chromatophores are responsive to change in background, extracellular pigment in the hypodermis and exoskeleton prevents the animal from effecting an immediate change in appearance. Hitchcock concluded that the pattern of the individual crab is probably genetic. Chace (1951) remarked that in view of these findings, the apparent color of any individual can be changed only at the time of molting.

Habitat.—These crabs are more abundant on *Sargassum* in the Sargasso Sea than elsewhere, but throughout their range they depend on flotsam, or on floating or swimming organisms to which they cling (Chace, 1951).

Type locality.—On sargasso and other submarine sea plants on the north side of Jamaica (Sloane *in* Holthuis, 1959).

Known range.—Atlantic Ocean south of Newfoundland, west of 50° W. latitude, and exclusive of the Gulf of Mexico (Chace, 1951); Netherlands coast, North Sea (van den Oord and Holthuis, 1959).

Remarks.—The genus *Planes* has been thoroughly reviewed by Chace (1951), and the serious student should consult this paper. Chace included remarks on relative growth, stating that . . .

> The carapace length-width relationship remains fairly constant with a slight tendency toward narrowing, from the smallest immature specimens examined to a carapace length of about 11 mm. At this stage the carapace seems to become somewhat narrower rather abruptly and continues to become narrower at a slightly more rapid rate than during the younger stages. A similar, but even more striking, trend is noticed in the relative shortening of the walking legs.

Chace conjectured that the specimens larger than about 11 mm. are found on flotsam and turtles rather than on sargassum, and that the shorter legs may be more adapted to this existence than to life on floating weed. It is also possible that these sizes represent different forms of *Planes* with somewhat different habits, but Chace deferred such a designation until a time when more material is available for study.

Both Hyman (1924b) and Lebour (1944) illustrated some larval stages of *Planes minutus*. In the region of the Carolinas, ovigerous females have been taken virtually throughout the year.

Subfamily **Varuninae**

Front moderately or little deflexed, sometimes sublaminar. Branchial region with downward sloping posterolateral portion set off from rest of region by a more or less distinctly marked line. Suborbital crest, supplementing defective lower border of orbit, rather distant from orbit and usually running in a line with anterior border of epistome. Antennal flagellum usually of good length. External maxillipeds moderately or slightly gaping, without oblique hairy crest; palp articulating with middle of anterior border or near anteroexternal angle of merus; exognath in American genera rather narrow, sometimes partly concealed. Male abdomen rarely covering all space between last pair of legs (Rathbun, 1918b).

Genus ***Euchirograpsus*** Milne Edwards, 1853

Rathbun, 1918b, p. 281—Hemming, 1958b, p. 31.

Euchirograpsus americanus Milne Edwards

Figure 204

Euchirograpsus americanus Milne Edwards, 1880, p. 18.—Rathbun, 1918b, p. 282, text-fig. 144, pl. 74.—Hay and Shore, 1918, p. 448, pl. 36, fig. 7.—Garth, 1946, p. 511, pl. 85, figs. 5–6.

Recognition characters.—Carapace slightly broader than long; sides nearly straight and parallel, flattened posteriorly, sloping gently down toward sides and front; surface covered with granules and short, soft hair. Front somewhat produced, lamellate, with a narrow median notch. Eyes large; orbits large, a small tooth at inner angle; upper margin oblique, sinuous; outer angle spiniform, behind it three smaller spines on lateral margin, middle spine largest; lower margin of orbit denticulate. Third article of antennae hollowed out on inner side.

Chelipeds stout, 1.5 times as long as carapace; merus with surface crossed by fine granulated lines, margins spinulose, a superior subdistal spine; carpus with inner distal margin spinulose; hand with three spinulose ridges above, a ridge near lower edge, and another less distinct through middle; fingers slender, grooved, pointed, gripping edges with low, irregular teeth fitting together. Walking legs slender, compressed, hairy; second pair over twice length of carapace; all meri crossed by fine granulated lines and with three subdistal spines, one above, one inner, and one outer below, first merus spinulose below; dactyls armed with long spines.

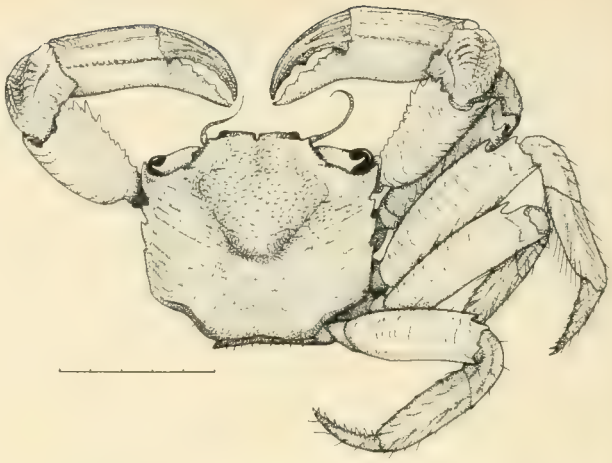

FIGURE 204.—*Euchirograpsus americanus* Milne Edwards. Animal in dorsal view, walking legs of left side not shown, 5 mm. indicated.

Measurements.—Carapace: female, length, 14 mm.; width, 16 mm.

Color.—Yellowish gray, arranged in marblings on carapace and in alternately light and dark bands on legs, or light brown with five or six bands of red on legs (various authors). More detail given by Garth (1946).

Habitat.—Seventeen to 278 fathoms.

Type locality.—Barbados, 69 fathoms, *Blake* station 278.

Known range.—Off Oregon Inlet, N.C., through West Indies to Barbados, and through Caribbean Sea to Monosquillo [Morrosquillo], Colombia; Galapagos Islands.

Remarks.—This species had rarely been taken off the Carolinas until recently. Offshore collecting has shown it to be not uncommon, and a northern, as well as upper bathymetric record, was established when an ovigerous female was taken off Oregon Inlet, N.C., at 17 fathoms in February (Cerame-Vivas, Williams, and Gray, 1963). Ovigerous females are otherwise known in Florida from March to September.

Subfamily **Sesarminae**

Front strongly deflexed. Lower border of orbit commonly running downward toward angle of buccal cavern. Side walls of carapace finely reticulated with granules and hairs or hairs only. External maxillipeds separated by a wide rhomboidal gap, an oblique hairy crest traversing them from a point near anteroexternal angle of ischium to a point near anterointernal angle of merus; palp articulating either at summit or near anteroexternal angle of merus; exognath slender and either partly or almost entirely concealed. Male abdomen either filling or not quite filling all space between last pair of legs (Rathbun, 1918b).

Genus ***Sesarma*** Say, 1817

Rathbun, 1918b, p. 284.

KEY TO SPECIES IN THE CAROLINAS

a. Lateral margin of carapace sinuous; last three articles of first three walking legs tomentose; body strongly convex above ..... *reticulatum* (p. 221).

aa. Lateral margin of carapace straight; walking legs not tomentose; body nearly flat above ... *cinereum* (p. 222).

Sesarma (Sesarma) reticulatum (Say)

Figure 205

Ocypode reticulatus Say, 1817, p. 73, pl. 4, fig. 6.
Sesarma reticulatum: Rathbun, 1918b, p. 290, pl. 77 (rev.).
Sesarma reticulata: Hay and Shore, 1918, p. 448, pl. 36, fig. 12 (rev.).

Recognition characters.—Carapace about four-fifths as long as broad, convex, regions distinct, surface punctate and with scattered clumps of setae above and in front; sides concave behind widest point, convergent at orbital angles. Posterolateral regions obliquely striated and setose; inferolateral and frontal regions with irregular rows of tubercles bearing short, curved hairs. Dorsal portion of carapace overhanging sides; beneath projecting shelf a line of cilia. Lower surface of carapace covered with fine net of geniculate hairs. Front broad, slightly sinuate above basal articles of antennae. Eyestalks short and stout, set in deep oval orbits; a deep gap below outer orbital angle leading into system of grooves opening into a notch at anterolateral angle of buccal cavern. External maxillipeds separated by a wide rhomboidal gap largely filled by a hairy fringe, and obliquely traversed by a conspicuous line of hairs from point behind anteroexternal angle of ischium to anterointernal angle of merus.

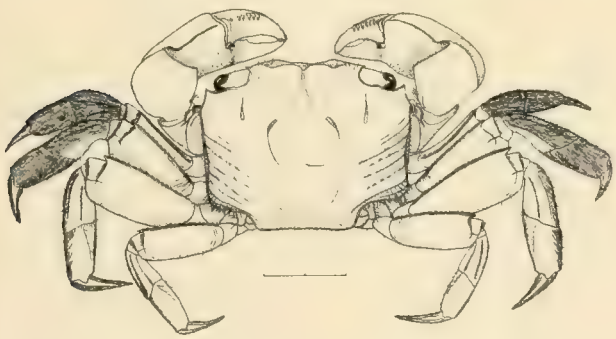

FIGURE 205.—*Sesarma (Sesarma) reticulatum* (Say). Animal in dorsal view, 10 mm. indicated.

Chelipeds stout, subequal in male; merus and carpus lightly rugose; merus with an obtuse subterminal tooth above, both lower margins denticulate; carpus with inner angle rounded. Palm almost smooth, in male a little higher than midlength, upper edge with a single granulate line, inner surface with a short irregular ridge of tubercles near distal end; dactyl with seven to nine depressed spinules above on basal two-thirds; fingers agape, an enlarged tooth near each end. Palm of female half again as high as midlength, fingers slightly agape. Third pair of walking legs approximately twice as long as carapace, last three articles densely tomentose.

Measurements.—Carapace: male, length, 23 mm.; width, 28 mm.

Color.—Carapace dark olive, nearly black or purple; dark plum colored or bluish-black speckles crowded on grayish background, grayish color showing little except on posterior part; upper part of chelipeds similarly colored but brighter, greater part of palm yellowish, tips of fingers white or yellowish; upper part of legs as carapace; under parts grayish (various authors).

Habitat.—Burrows in muddy salt marshes.

Type locality.—Muddy salt marshes [east coast of United States].

Known range.—Woods Hole, Mass., to Calhoun County, Tex.

Remarks.—Ovigerous females have been reported from Massachusetts in July, and in summer months farther south on the coast. Crichton (1960) found 8,000 to 10,000 eggs per egg mass.

Hyman (1924b) described the first zoeal stage and compared it with *S. cinereum.* Recently, Costlow and Bookhout (1962a) described the complete

larval development listing three zoeal stages and one megalops stage, and compared these to similar stages they had previously described for *S. cinereum*. The authors also concluded that photoperiod has no observable effect on development.

Crichton (1960) studied a colony of *S. reticulatum* in Delaware. With the aid of rubber casts, he found that the species digs burrows which may have several openings leading at a gentle slope to a depth of 3 or 4 inches where a series of more or less level corridors curve, twist, and often interconnect. Each corridor usually leads to a vertical shaft as much as 30 inches deep and usually filled with water. Burrows are communal, containing a male or two and several females. Crichton found that this species will eat fiddler crabs (the burrows occasionally intersect) when it can capture them; however, the usual diet is *Spartina*, and swaths often are cut through this marsh grass. Burrowing action of the crab tills the land, increases erosion, and turns over the cord grass more rapidly than the annual decay cycle could do it unaided.

Teal (1959) found this species active on Georgia marshes when the tide was high or the sky cloudy. When the marsh was exposed, the crabs were found in burrows, usually near the top, in air or water. Respiration rates were higher in water than in air. Gray (1957) found the gill area of *S. reticulatum* to be relatively low as compared with other species living in a similar habitat (*Uca pugnax* and *minax*). He found *S. reticulatum* to be more robust but less active than the close relative, *S. cinereum*.

Humes (1941) described a harpacticoid copepod (*Cancrincola plumipes*) from the gill chambers of this crab.

Sesarma (Holometopus) cinereum (Bosc). Wharf crab; wood crab; friendly crab; square-backed fiddler

Figure 206

Grapsus cinereus Bosc [1801 or 1802], p. 204, pl. 5, fig. 1.
Sesarma cinereum: Rathbun, 1918b, p. 300, text fig. 149, pl. 83 (rev.).
Sesarma cinerea: Hay and Shore, 1918, p. 449, pl. 36, fig. 11.

Recognition characters.—Carapace rectangular, nearly uniform in width throughout; regions well marked; surface nearly smooth, punctate, rough with subuniform tubercles toward front; suprafrontal lobes well marked, inner pair widest. Front [illegible] as wide as high, widening below,

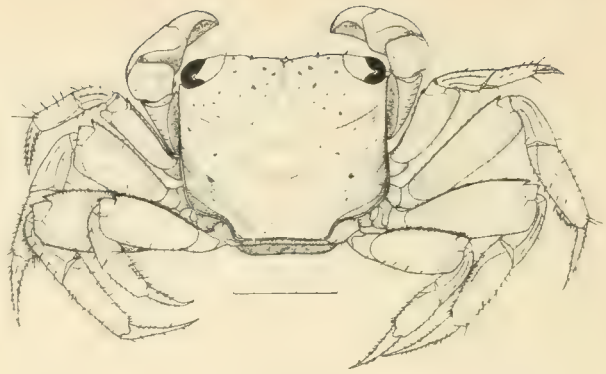

FIGURE 206.—*Sesarma (Holometopus) cinereum* (Bosc). Animal in dorsal view, 5 mm. indicated.

somewhat four-lobed in dorsal view, lower edge sinuous. Outer orbital angle acute. Lower surface of carapace covered with fine net of geniculate hairs.

Chelipeds heavy; merus and carpus covered with short transverse lines of scabrous granules; merus with upper edge sharp, inner edge irregularly dentate with a triangular laminar expansion on distal half; carpus with inner angle rounded. Palm nearly twice as high as upper length; outer surface covered with scabrous granules arranged in parallel lines near upper margin; inner face coarsely granulate, with short prominent ridge near distal end; fingers gaping narrowly, largest tooth at middle of immovable finger. Walking legs rather narrow, meri with a superior subdistal spine; third pair of legs over twice as long as carapace.

Abdomen of male broadly triangular; telson much narrower than sixth segment.

Measurements.—Carapace: male, length, 18 mm., width, 20 mm.; female, length, 20 mm., width, 23 mm.

Color.—Brown varying toward olive.

Habitat.—Found actively crawling about on wharves and stone jetties or resting in shallow burrows above tidemark along the shores. The crabs have often been found on vessels along the coast hiding anywhere out of sight or reach and coming forth at night to feed.

Type locality.—"*La Caroline.*"

Known range.—Magothy River, Chesapeake Bay, Md., to British Honduras; West Indies to Venezuela.

Remarks.—This species is abundant where it occurs in the Carolinas. Ovigerous females occur

from May to November in North Carolina, and have been found along the Potomac River in January (U.S. National Museum records). Hyman (1924b) briefly described the first zoeal stage. Costlow and Bookhout (1960) described 4 zoeal stages and 1 megalops stage from 1,200 zoeae reared on *Artemia* nauplii and *Arbacia* eggs under constant conditions of temperature, salinity, and light. Costlow, Bookhout, and Monroe (1960) found that optimum salinities exist for each larval stage, but that development proceeds best in the 20–26.7 °/₀₀ range (among those tested). Temperature was found to have more effect on length of larval development than on mortality, with higher temperature speeding development. No "extra stages" were observed. The authors concluded that salinity is the chief physical factor confining *S. cinereum* to estuaries.

Pearse (1929) found that this species can survive for a considerable period of time in dilutions of sea water and also that it shows considerable resistance to desiccation. Oler (1941) maintained captive specimens from a Maryland tidal river in a house basement for about a year. The animals burrowed in mud in an aquarium where the only moisture provided was tap water. Vegetable matter was fed at irregular intervals. After several months, the larger animals ate the smaller ones, presumably at the time of ecdysis. Duncker (1934), in Germany, secured three live female *S. cinereum* which had been transported by chance in a cargo of logs from the West Indies. The animals were kept alive in a glass jar with damp peat and a container for a source of fresh water. One lived 4 years and 72 days from date of captivity. The crabs were fed shredded beef or fish and commercial fish food plus Collembola that appeared in the jar. All eating was done on land. Some regeneration of lost appendages occurred, and the longest lived specimen molted four times, molting always taking place in water. To the author's surprise, eggs were released six times, always in water, the longest lived female producing five of these batches. Larvae hatched from all but one of the egg masses, but survived only a short time. Duncker concluded that one mating was effective for 3 years or more. The incubation period was approximately 30 days. The female ate eggs that protruded over the edge of the abdomen. The number of eggs ranged from about 4,700 to 13,400 per sponge. Duncker considered that *S. cinereum* acted more like a land animal than a water-inhabiting animal, each individual having its own burrow.

Teal (1959) implied the same conclusion, for in experiments under water this species was relatively inactive, thus holding its oxygen consumption down. There was some experimental evidence for thermal acclimation of metabolism, but more evidence for acclimation by selection of microclimate. Gray (1957) also emphasized the terrestrial habits of the species, but showed that its relative gill area is nearly double that of the similar species *Ocypode quadrata*.

Subfamily **Plagusiinae**

Front cut into lobes or teeth by antennular clefts visible in dorsal view. Lower border of orbit curving down into line with prominent anterior border of buccal cavity. External maxillipeds neither completely closing buccal cavity nor leaving wide rhomboidal gap, not crossed by an oblique hairy crest; palp articulating near anteroexternal angle of merus, often no flagellum on exposed exognath. Antennal flagella short. Male abdomen filling all space between last pair of legs (Rathbun, 1918b.).

Genus ***Plagusia*** Latreille, 1804

Rathbun, 1918b, p. 331.—Monod, 1956, p. 455.

Plagusia depressa (Fabricius)

Figure 207

Cancer depressus Fabricius, 1775, p. 406.
Plagusia depressa: Rathbun, 1918b, p. 332, text-fig. 154, pl. 101 (rev.).—Monod, 1956, p. 455, figs. 614–617 (rev.).

Recognition characters.—Carapace subhexagonal, wider than long, depressed, covered with flattened tubercles margined with short setae. Regions distinct; front of gastric region with a series of approximately six, prominent, acute tubercles arranged in an arc. Indefinite front broad, with a deep median furrow and deep notches for antennules; a spiniform tubercle on each side between median furrow and antennulary notch. Orbits deep; outer orbital angle produced into a strong, curved spine followed on anterolateral margin by three similar spines of diminishing size. Epistome prominent beyond anterior border of carapace and usually cut into five lobes.

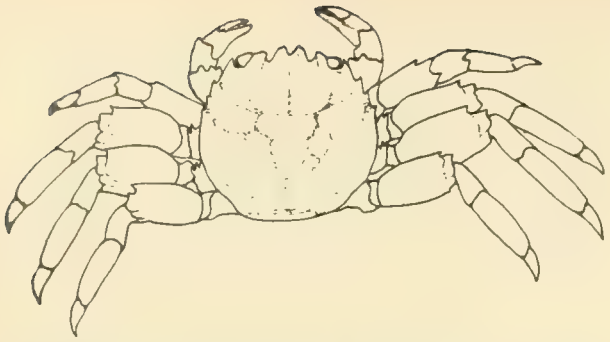

FIGURE 207.—*Plagusia depressa* (Fabricius). Animal in dorsal view (after Rathbun, 1933).

Chelipeds of adult male massive, approximately as long as carapace, in female slender, three-fourths as long as carapace; chelipeds and legs rugose dorsally; merus with three small spines above at distal end; carpus with inner angle densely dentiform; palm and dactyl with tubercles arranged in longitudinal ribs, outer surface smooth. Walking legs strong, increasing in size from first to third, fourth shorter than second; second and third legs with a dentate crest above on coxae; meri with subterminal spine on anterior border; distal three articles with a dense strip of long hair; dactyls with two rows of strong spines on concave side.

Measurements.—Carapace: large female, length, 45 mm.; width, 49 mm.

Color.—Light reddish, dotted with blood red, tubercles bordered with blackish cilia with extremity gray; blood-red spots on legs; underside of body yellowish (Latreille *in* Rathbun, 1918b).

Habitat.—This species is found among rocks, on jetties, in tide pools, and is thought to be transported on ships' hulls.

Type locality.—"*In mari mediterraneo.*"

Known range.—Beaufort, N.C. through West Indies to Pernambuco, Brazil; Bermuda; Azores; Madeira; West Africa, from Senegal to Gold Coast.

Genus ***Percnon*** Gistl, 1848

Rathbun, 1918b, p. 337.—Hemming, 1958b, p. 35.

Percnon gibbesi (Milne Edwards). Spray crab

Leucothocarpus gibbesi Milne Edwards, 1853, pp. 146 and 180.
Percnon gibbesi: Rathbun, 1918b, p. 337.—Schmitt, 1939, p. 24.

Recognition characters.—Carapace thin, disclike, longer than wide, covered with small short bristles except for bare raised patches; dorsal surface with a few low tubercles. Front deeply cut by antennular furrows; portion between antennules narrow and extended in form of a rostrum, armed with two erect spines on each side distally and a row of inconspicuous spinules just within and parallel to each margin proximally. Eyes large, reniform. Inner margin of orbit bearing three spines, two distal spines prominent; middle of upper orbital border more or less serrate. Anterolateral border of carapace with four acute spines counting large spine on outer orbital angle; second spine in series with its lateral margin shorter than that of third spine.

Chelipeds varying in size with age and sex, small in females but large and unequal in adult males; merus and carpus armed with spines; palm nearly smooth, oval, and somewhat compressed, proximal upper surface with an ill-defined groove extending one-third length of upper margin, groove filled with pubescence; fingers short, blunt, with tips concave on opposed surfaces. Meral article of each walking leg with large uniform spines on anterior margin, upper surface covered with short bristles similar to carapace; posterior margin ending in a distal spine; merus of first two legs with a second row of spinules parallel with anterior border, row indistinct on third merus and absent on fourth.

Measurements.—Carapace: male, length, 30 mm., width, 28 mm.; female, length, 33 mm., width, 34 mm. (Garth, 1946).

Color.—Carapace and meral articles of walking legs brown or mottled above; usually a median longitudinal stripe of white or pale blue; legs banded with reddish, brown, and light pink distally; eyestalks and chelae orange; ventral side of body pale blue with legs pale pink (Garth, 1946; Verrill, 1908).

Habitat.—The usual habitat for this species is the underside of rocks at the low-tide level (Verrill, 1908), or in the surf at knee to hip depth, where it is extremely difficult to capture because of its propensity for rapidly keeping to the underside of turned objects (Garth, 1946).

Type locality.—Antilles.

Known range.—Fort Macon, N.C.; southern

Florida and Bahamas to Brazil; Bermuda; Azores to Cape of Good Hope; Cape San Lucas, Lower California, to Chile; Galapagos Islands.

Remarks.—Two immature females found on the Fort Macon, N.C., jetty in August 1963, by R. A. Heard, are referred to this species on the basis of characters given by Schmitt (1939) in his key to species of the genus *Percnon*. It is impossible to refer the descriptions of Rathbun (1918b) and Verrill (1908) to this species or *planissimum* with certainty, and the figures given by them also are not adequate for this purpose; but on the basis of a Bermuda specimen collected in 1962, Verrill's material was probably *P. gibbesi*.

Failure to record this species from North Carolina prior to this time is probably because there are few suitable habitats along this coast. There are few natural rocks on the North Carolina coast.

Family **Ocypodidae**

Palp of external maxillipeds coarse, articulating at or near anteroexternal angle of merus; exognath generally slender and often somewhat concealed. Front usually of moderate width, and often a somewhat deflexed narrow lobe. Orbits occupying entire anterior border of carapace outside front, and with their outer wall often defective. Buccal cavity usually large and somewhat narrower in front than behind, external maxillipeds often, but not always, completely closing it. Abdomen of male narrow. Male openings sternal (Rathbun, 1918b).

Genus ***Ocypode*** Weber, 1795

Rathbun, 1918b, p. 366 (described).—Monod, 1956, p. 390 (synonomy).

Ocypode quadrata (Fabricius). Ghost crab; sand crab

Figure 208

Cancer quadratus Fabricius, 1787, p. 315.
Ocypode albicans: Rathbun, 1918b, p. 367, pls. 127–128 (rev.).—Hay and Shore, 1918, p. 450, pl. 37, fig. 1.
Ocypode quadrata: Holthuis, 1959, p. 259.

Recognition characters.—Carapace quadrilateral, convex above from front to back, sides nearly vertical; dorsal region finely granulate on middle and posterior portions, coarsely granulate toward sides, center of carapace with a well-marked H-shaped depression. Front and side margins raised, beaded, or serrulate, lateral margin continued into

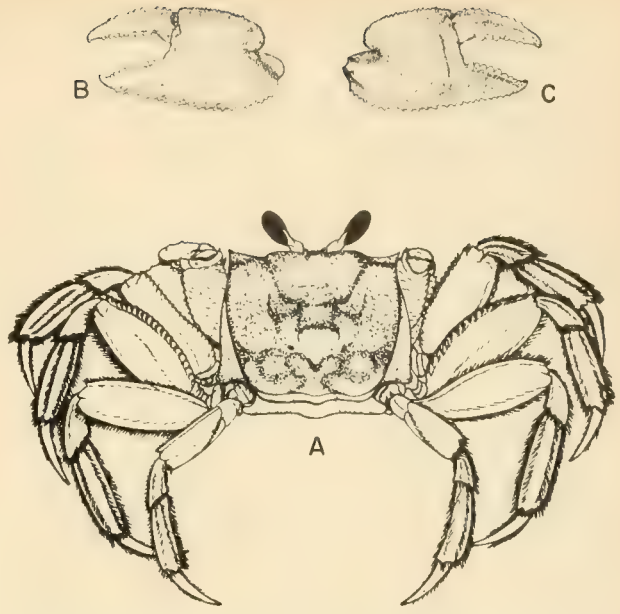

FIGURE 208.—*Ocypode quadrata* (Fabricius). A, female in dorsal view, reduced (after Gmitter and Wotton, 1953); major chela of male, B, outer view, C, inner view, reduced (after Crane, 1941).

a prominent, acute angle at outer corner of orbit; a similar but lower ridge extending upward and forward from base of third walking leg. Orbits large and open, extending all along anterior margin on either side of narrow front, both upper and lower margins crested and dentate. Eyestalks large, club-shaped, cornea covering over half of distal article. Front deflexed; antennules and antennae much reduced, flagellum of antennules hidden beneath front.

Chelipeds in both sexes, and in young, unequal, well developed, rough; merus serrulate above, toothed on lower margins; carpus with sharp spines at inner angle; hands coarsely scabrotuberculate, margins of palm and fingers dentate, fingers pointed. Large hand with a vertical stridulating ridge of tubercles on inner surface near base of movable finger that plays against smooth, distal, anteroventral ridge of ischium. Walking legs almost smooth, fringed with long, stiff, yellow hair, third pair longest, fourth shortest; meri of first three pairs broadened; propodi of these legs with longitudinal brushes of hair on anterior surface; dactyls of all legs fluted, depressions hairy.

A hair-fringed breathing slit on ventral surface between basal articles of third and fourth walking legs.

Measurements.—Carapace: male, length, 44 mm.; width, 50 mm.

Color.—Gray, pepper-and-salt, grayish white, pale yellow, straw color, or yellowish white imitating color of beaches; sometimes light amber and often iridescent; yellow markings below and and on legs; young mottled gray and brown (various authors).

Habitat.—This species, the most terrestrial of the decapod crustaceans in the Carolinas, lives in abundance along the ocean beaches and sometimes on harbor beaches. The crabs construct burrows 2 to 4 feet in depth from near the high-tide line to distances up to a quarter of a mile from the ocean.

Type locality.—Jamaica.

Known range.—Block Island, R.I., to State of Santa Catarina, Brazil (megalops have been taken at Woods Hole).

Remarks.—The ghost crabs are so large, accessible, and widely distributed that they have been extensively investigated in various parts of their range.

Perhaps because of its mode of life, this animal has left a fragmentary fossil record. Rathbun (1935) recorded *O. quadrata* questionably from the Pleistocene of Florida. Hayasaka (1935) compared the "sandstone pipes" commonly found in certain Tertiary sandstones of Formosa to plaster casts of burrows made by the Formosan crab, *O. ceratophthalma*, and found them to be much alike. Burrows of the modern Formosan and eastern North American species are similar.

The egg-laying season in the Carolinas appears to extend from April (Coues, 1871) to July. Apparently the egg-bearing period is approximately the same farther south at Tortugas, Fla. (Cowles, 1908), and farther north in New Jersey (Milne and Milne, 1946). The latter authors pointed out that ovigerous females differ in behavior from other individuals in that they wade in water more freely, run along on the bottom, and at intervals when the water is quiet open the abdomen out, flip upside down, extend the mouthparts, rotate the legs, and, thus, force water through the egg mass. Such females will run quickly to water when disturbed. The free-swimming zoea of this species has not been described, but the megalops was first described by Say (1817) as *Monolepis inermis.* Smith (1873a, 1873b, 1880b) recognized the true status of the form, and pointed out that though this megalops is carried as far north as Vineyard Sound by the Gulf Stream, that area is apparently too cold to support an adult population.

Habits of *O. quadrata* have been treated in a number of scholarly and popular works, but the serious student is referred especially to Cowles (1908) and Milne and Milne (1946). A popular account of some value, except for the concluding conjectures, was given by Phillips (1940). Only a brief summary from these authors can be given here.

The young crabs are found close to shore. Burrows of the young are near the water and extend to water level or are covered by high tides for a time, whereas older crabs burrow farther from water; such burrows seldom are deep enough to reach water level. Burrows are of three general types: (1) a short vertical burrow made by young crabs, (2) a burrow sloped downward at about 45 degrees away from the shoreline, often with a vertical branch extending upward almost to the surface, and (3) burrows higher on the beach, much like the second type but without the vertical side branch. In fall in New Jersey, the burrows were found to be farther from water and far deeper than any studied earlier in the year, and it is presumed that a variety of sizes of crabs hibernate in these deep burrows.

Burrow making is primarily an occupation of daylight hours. The crabs cease feeding on the wet beach toward dawn. Those feeding on a fish carcass often burrow within an inch or two of the carcass. Young crabs near water make new burrows, older ones range inland and build burrows or occupy old holes. Sand is brought to the mouth of the burrow and dropped or spread near the opening in a fan-shaped area. Toward noon, openings to burrows are plugged with damp sand, thus concealing the burrow. Toward evening the crabs begin to emerge again, and by 10 p.m. the whole population is usually on the beach.

These crabs are scavengers (and cannibals) and tend to feed most actively along the drift line, looking for beached fish or refuse and small bits of food buried in the top layer of sand. The crabs

do not enter the water to search for or capture food.

The crabs have to go into the water at intervals to moisten the gills, and the young do this more frequently than adults. When undisturbed, the individuals do not actually enter water but will stop a few inches from the waterline with one side presented to the water, the legs of the other side anchored in sand, and wait for a wave to wash over them after which they return to the higher parts of the beach. If disturbed, the crabs will run into the water, then leave it as soon as possible. These crabs do not swim but walk on the bottom or are rolled about by waves. The crabs can survive for a limited time if forced to remain submerged.

Locomotion is accomplished by all eight walking legs. Usually the crabs walk sideways or obliquely. If hotly pursued, the crabs will run in another manner, holding the last pair of legs clear of the ground. Usually the crabs walk or run toward the side with the small chela. This crab can also walk forward, or sometimes approach food by walking slowly backward.

The eyes of *O. quadrata* are so large and prominent that it seems as if the crab can see exceptionally well. Experiment has shown that the eyes are primarily sensitive to large changes in intensity of light. The crabs do not tend to avoid strong light, but try to hide if lights are suddenly shut off or if an object on the beach is suddenly moved. The eyes apparently aid in the search for food, but actual detection of food is by taste or smell.

There is no evidence that *O. quadrata* can hear, though a well-developed stridulating ridge is borne on the large chela. No one has reported observing this crab in the act of stridulating.

Cowles (1908) noticed that the ghost crab exhibits color changes. The crabs are generally dark in subdued light and in direct sunlight if temperature is not above 35° C. Above 35° C., the crabs are light colored regardless of light intensity. In absence of light, the crabs are light colored regardless of temperature.

The general relationship of habitat to oxygen consumption and general activity among certain decapods has been a subject of study by Ayers (1938), Pearse (1929), Vernberg (1956), and Gray (1957) in the Beaufort, N.C., area. In all these studies, *O. quadrata* was of prime interest because of its terrestrial adaptation combined with great activity. Of all the crabs studied in this geographic area, the ghost crab possesses the highest rate of oxygen consumption both for the whole animal and for gill tissue alone. This is more striking when it is emphasized that *O. quadrata* has a reduced number of gills (though it does have accessory respiratory tissues in the gill cavity) and the gill area per gram of weight in this species is by far the lowest among 16 species studied in near-shore, intertidal, and above-tide zones.

Flemister and Flemister (1951) and Flemister (1958) have shown that when *O. quadrata* is confined in water, oxygen consumption is elevated, but elevated least when chloride ion concentration of the water equals that of the blood. Lower or higher ion concentration of the water raises the respiration rate. They demonstrated that the animals normally have blood hypotonic to sea water. In sea water containing less than 120 or more than 160 millimoles of chloride per liter, the internal concentration is not maintained but tends to rise or fall depending on which end of this range the animal experiences. The antennal gland, aided by the gill membranes, functions in regulation of internal chloride ion concentration.

Genus *Uca* Leach, 1814

Rathbun, 1918b, p. 374.—Monod, 1956, p. 399.

KEY TO SPECIES IN THE CAROLINAS

a. Large cheliped of male with oblique tuberculate ridge on inner surface of palm extending upward from lower margin.
  b. A prominent transverse depression behind orbit; leg joints red on large cheliped; color dark, usually grayish toward front margin ..... *minax* (p. 227).
  bb. Without prominent transverse depression behind orbit; leg joints not red; color dark, often with blue on front ..... *pugnax* (p. 229).
aa. Large cheliped of male without oblique tuberculate ridge on inner surface of palm extending upward from lower margin ..... *pugilator* (p. 232).

Uca minax (Le Conte). Red-jointed fiddler; brackish water fiddler

Figures 209A, 210B

Gelasimus minax Le Conte, 1855, p. 403.
Uca minax: Rathbun, 1918b, p. 389, pl. 137 (rev.).—Hay and Shore, 1918, p. 451, pl. 37, fig. 3.

Recognition characters.—Carapace subquadrilateral, approximately 1.3 times as wide as long, widest behind outer orbital angles, convex in both

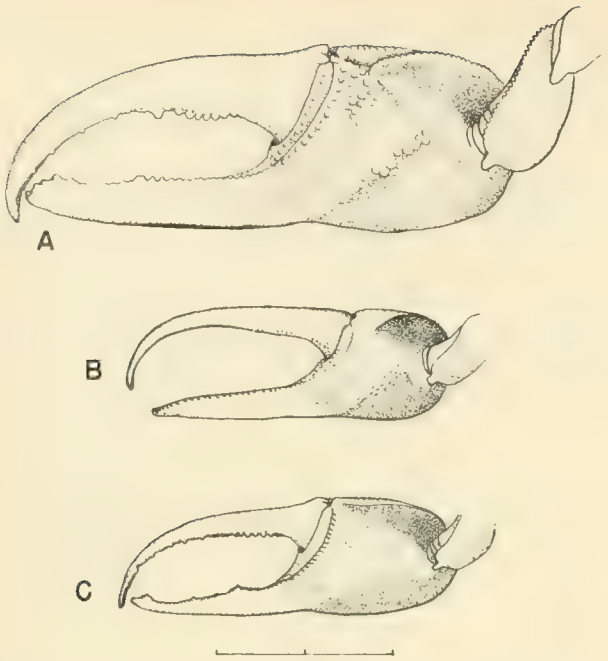

FIGURE 209.—Large chela of male, view of inner side; A, *Uca minax* (Le Conte); B, *Uca pugnax* (Smith); C, *Uca pugilator* (Bosc); 20 mm. indicated.

directions, finely granulate, except somewhat coarsely so near anterolateral angles; a shallow H-shaped depression near center of carapace, and a horizontal depression behind orbit. Lateral margins nearly vertical; anterolateral angles slightly produced, continued backward and inward as a low, well-defined ridge, and above orbits as a low revolute ridge. Front greater than one-third frontoorbital width, broadly convex. Orbits large, open, eyebrow 5 times as wide as deep, lower margin dentate; eyestalks long, slender. Antennules and antennae small, flagellum of antennules hardly visible. Merus of second maxilliped with never more than 10 exceedingly slender spoon-shaped hairs.

Chelipeds in male very unequal, in female equal and of small size. Large chela with upper surface of merus sparingly granulate, inner edge denticulate, outer edge granulate; carpus tuberculate. Upper and outer face of large hand in male with tubercules diminishing to granules on lower face, ridged above; inner surface with an oblique row of granules from lower margin to carpal cavity, [illegible]ort curved row leading down from ridge on upper margin, area between ridges tuberculate and with a tuberculate ridge running along immovable finger from tip to internal distal border of palm. Fingers strong, with wide gape, cutting edges tuberculate; immovable finger with a few larger teeth at irregular intervals, truncate at tip; dactyl longer and curving downward past tip of opposed finger. Walking legs strong, sparsely hairy, meri slightly wrinkled.

Measurements.—Carapace: male, length, 25 mm.; width, 38 mm.

Color.—Chestnut brown, becoming gray in front; chelipeds with red spots at articulations; hands ivory white; legs olive or grayish brown.

Habitat.—This species occurs in marshes at some distance from water of high salinity. It is usually found on muddy substrates where flooding with fresh water occurs (Teal, 1958), or on a mud and sand substrate (Gray, 1942). In North Carolina, the species is found in *Spartina* marsh, often far from banks of ditches, and in the area immediately preceding the *Salicornia-Distichlis* zone (Vernberg, 1959). It has also been observed at the edge of low woodlands (Teal, 1959). The crabs live in burrows which they dig to various depths, but the maximum is about 2 feet. The openings are often considerably above high-tide level, and the bottoms reach to ground-water level. The burrows are only wide enough to accommodate the occupant. Usually only one crab lives in a burrow, though at times two females may occupy a single burrow, and burrows of females sometimes communicate with burrows of males, the connection being made by the female (Gray, 1942). Young crabs are sometimes found in the burrows of females, never in those of males.

Type locality.—Beesleys Point, N.J.

Known range.—Buzzards Bay (Wareham), Mass., to Matagorda Bay, Tex.; Colombia; Dominican Republic.

Remarks.—This species has been the subject of a number of ecological and physiological studies, undoubtedly because of its wide distribution and accessibility. It is the largest of the three species of fiddler crabs occurring on the east coast of the United States, though it is not so abundant as the other two species and its habitat is somewhat more restricted.

Spawning occurs in the Carolinas and as far north as mid-Chesapeake Bay in summer. In Chesapeake Bay, ovigerous females are most

abundant in July; none are known to occur before July or after the first week in September, and about the same length of breeding season is found in the Beaufort, N.C., area. Gray (1942) presented evidence for two spawnings per season. The act of egg laying has not been studied in minute detail, but Gray (1942) observed egg deposition among captive females held in aquaria. Completion of spawning was usually accomplished in a day but sometimes took as long as 3 days, depending on temperature. (Hyman (1920) and others have dug ovigerous females from burrows.) Freshly laid eggs were yellow or pale orange in color, but the color changed with development through a purplish-black to an ashy gray color, at which stage the larvae emerged (see also Hyman, 1920). Estimated egg counts on a number of ovigerous females ranged from 10,000 to 300,000, depending on size of the individual. Newly laid eggs measured about 0.09 mm. in diameter but increased to about 0.27 mm. at the time of hatching. Both Hyman (1920) and Gray (1942) observed that the females entered water in order to let the eggs hatch. Time of hatching extended from about 7:00 to 10:00 p.m., and the hatching of an egg mass required slightly less than an hour.

The first zoeal stage of *U. minax* is the smallest among our three species of *Uca*. The larval stages are discussed in the remarks on *U. pugilator*.

Uca minax is an omnivorous feeder but avoids highly putrified debris (Gray, 1942). Teal (1958) showed that fiddler crabs can subsist on a mixture of sand, clay, bacteria, and fermented marsh grass (natural staples in their diet), and he observed *U. minax* kill and eat *U. pugnax* and *U. pugilator* on several occasions. Contrary to the findings of others, he observed (1959) that *U. minax* can and does feed underwater. Miller (1961) compared the mouthparts of *U. minax* to those of the more specialized Carolinian *Ucas*. He found that it prefers to feed in low areas of the *Spartina* marshes well up in estuaries where mud is fluid.

In a search for factors that might limit *U. minax* to its particular habitat, Teal (1958) found that the temperatures experienced in nature had no effect on survival but that the species could live in fresh water for more than 3 weeks and, when offered fresh and salt water, *U. minax* chose to live in fresh water. When offered a choice of mud or sand substrates, this species chose mud either above or under water, but when competitive species of *Uca* were present fewer burrows were dug. Teal (1959) found that *U. minax* had the lowest rate of oxygen consumption among a number of marsh crabs investigated (*U. pugnax* and *pugilator*, *Sesarma cinereum* and *reticulatum*, *Eurytium limosum*, and *Panopeus herbstii*) which is contrary to the argument of Ayers (1938) that the more terrestrial species have relatively higher rates of metabolism than do aquatic forms. Teal (1959) and Vernberg (1959) further observed that *U. minax* in all probability does not acclimate respiratory rate to changes in temperature. Gray (1957) found gill area per gram of body weight in *U. minax* lowest among East Coast *Ucas*, Below 20° C., this species is inactive (Gray, 1942; Teal, 1959). Gray found that *U. minax* overwinters in burrows just below the frost line.

Sexual display of the males among fiddler crabs has been a subject of much study and is too complex for complete review here. Crane (1943, 1944) dealt with this subject briefly for *U. minax*. In display, the males rear back on the last two or three walking legs so that the carapace is vertical. The major cheliped is extended diagonally up to about half of maximum extension. This position may be held for minutes, then the cheliped may be fully extended swiftly and smoothly, and finally brought back to the half-extended position in a series of jerks. This movement may be repeated about four times rather slowly. The small cheliped is moved asynchronously in similar motions.

Uca pugnax (Smith). Mud fiddler

Figures 209B, 210A

Gelasimus pugnax Smith, 1870, p. 131, pl. 2, fig. 1, pl. 4, figs. 2–2d.

Uca pugnax: Rathbun, 1918b, p. 395, pl. 139.—Hay and Shore, 1918, p. 451, pl. 37, fig. 4.—Tashian and Vernberg, 1958, p. 89 (rev.).

Recognition characters.—Carapace subquadrilateral, approximately 1.5 to 1.75 times as wide as long, widest behind outer orbital angles, very convex anteroposteriorly, lower edge of front and upper margin of orbit invisible in dorsal view, smooth. A shallow H-shaped depression near center of carapace, a pit on branchial region in line with gastro-cardiac sulcus, and a pit behind mid-

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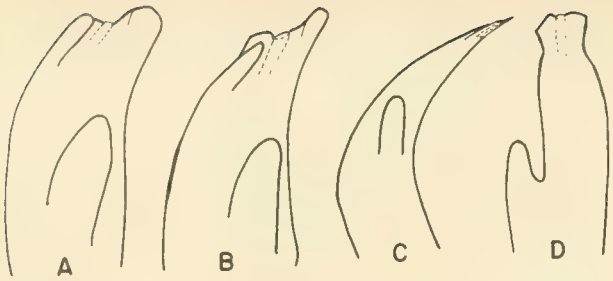

FIGURE 210.—Tips of right abdominal appendages of adult males, hairs omitted; A, *Uca pugnax*, anterior view; B, *Uca minax*, anterior view; C, *Uca pugilator*, anterior view; D, same, lateral view (after Crane, 1943).

dle of orbit. Anterolateral angles slightly produced, continued backward and inward as a low, well-defined ridge, and across entire frontoorbital width. Front about two-sevenths of frontoorbital width, margin regularly arched. Orbits large, open, upper margin sinuous and oblique, lower margin dentate. Eyestalks long, slender. Antennule and antenna small. Merus of second maxilliped with between 10 and 20, rarely 25, spoon-tipped hairs.

Chelipeds in male very unequal, in female equal and of small size. Large cheliped of male rough; merus with granulated rugose lines outside, lower margins granulate. Carpus and palm tuberculate outside; inner surface of palm with oblique row of granules leading from lower margin to carpal cavity; a short row leading down from ridge of proximal half of upper margin; area between crests coarsely granulate or tuberculate and with tuberculate ridge running along finger from tip to internal distal border of palm. Fingers long, slender, widely gaping; immovable finger usually with one large tooth near middle, inferior border nearly straight, tip sometimes depressed, truncate; dactyl evenly denticulate and with irregularly placed large tubercles, strongly curving downward past tip of opposed finger. Walking legs with carpal and propodal articles hairy.

Measurements.—Carapace: male, length, 15 mm.; width, 23 mm.

Variations.—There is a tendency toward decrease in size in the southern extremity of the range (Tashian and Vernberg, 1958).

Color.—Carapace of male dark greenish olive, middle and anterior portion mottled with grayish white; front variably light blue between and above bases of ocular peduncles, margin tinged with brown; large cheliped lighter than carapace, pale brownish yellow at articulations and along upper edge of dactyl, fingers nearly white along opposed edges; ocular peduncles and eyes much like dorsal surface of carapace; smaller cheliped and legs somewhat translucent and thickly mottled with dark grayish olive; sternum and abdomen mottled ashy gray. Females less mottled with white dorsally, and without blue on front (various authors).

Habitat.—Pearse (1914) recorded this species as living primarily on intertidal flats of mud or clay among the roots of *Spartina*, but overlapping to some extent the sandier habitat frequented by *U. pugilator*. He found the maximum number of burrows about 2 feet below high-tide mark, and often the burrows had mud towers at the mouths when the beach was littered with debris. Crane (1943) observed "shelter building" in this species to be in its most rudimentary form among the *Ucas*. She found that in a mixed population of *U. pugnax* and *U. pugilator*, *U. pugnax* always chose the side of any surface irregularity for a hole entrance in preference to flat ground. Pearse (1914) found burrows extending to 2 feet in depth and terminating at the water level. Teal (1958) reported burrows on Georgia Sea Islands to be in situations similar to those observed by Pearse, on low levees bordering tidal creeks or farther from creeks in firm, marshy ground sometimes covered only at spring tides. Schwartz and Safir (1915) found *U. pugnax* burrows on a muddy substrate well shaded by marsh vegetation; hence, continually moist. *U. pugnax* digs most actively when the tide is falling, and often hastens to plug burrows when the tide is rising to cover the burrow mouths (Pearse, 1914).

Type locality.—New Haven, [Conn.].

Known range.—Cape Cod, Mass., to near St. Augustine, Fla. (Tashian and Vernberg, 1958); northwest Florida to Texas (Hedgpeth, 1950).

Remarks.—Like the preceding species, *U. pugnax* is an abundant and easily accessible, relatively large decapod which has received the attention of numerous students. Only information of greatest general interest can be mentioned here.

The fossil record for this species extends only into the Pleistocene of New Jersey and Delaware (Rathbun, 1935).

Ovigerous females have been observed near Woods Hole, Mass., from July 4 to July 15 (Pearse, 1914), wandering about over the ground. Farther south the spawning season is more extended, from early July to mid-August in New Jersey (Crane, 1943), and as early as May 21 at Long Lake, Tex. (Hedgpeth, 1950), and in April in northeastern Florida (U.S. National Museum records). On Long Island, N.Y., the peak of spawning occurs in August (Schwartz and Safir, 1915). Crane (1943) thought it likely that in the region near New York two breeding times occur, one in July and the other in August.

The larval and postlarval stages are discussed in the remarks on *U. pugilator*. Hyman (1920) secured ovigerous females for hatching of eggs by digging them from burrows. He found the first zoea of *U. pugnax* to resemble closely that of *U. pugilator* except for smaller size of the former.

Schwartz and Safir (1915) found the food of *Ucas* to consist largely of minute algae left on sand by the outgoing tide. Such algae were picked up by means of the small cheliped in males; females, using both small chelae, secured more food in a given time than males. The small chelipeds seemed sensitive to such food, for they were dragged along on the sand while the animals searched for food. Much sand was taken up with the food. Rapidity of movement of the small chelipeds to the mouth was timed and found to be from 24 to 26 times a minute in males, and from 74 to 92 times per minute in females. Teal (1958) found that *U. pugnax* frequently feeds underwater, and that it often remains outside burrows and feeds as the tide rises. This species can subsist on bacteria and organic debris. Miller (1961) in his well-illustrated study considered *U. pugnax* to be intermediate in development of spoon-shaped hairs on the mouth parts and, therefore, more ubiquitous in choice of feeding substrates than its congeners in the Carolinas. Great detail is given in this study.

In experiments on salinity tolerance, Teal (1958) found that 50 percent of *U. pugnax* placed in fresh water died within 1.5 days. In water of 7 °/₀₀, 50 percent mortality occurred after 3 days. Given a choice of fresh or 30 °/₀₀, *U. pugnax* chose salt water. Teal concluded that these data are consistent with the general distribution of the species, which is restricted to tidal marsh.

Given a choice of sand or mud substrate above or under water, *U. pugnax* burrowed only in mud without any reference to water level, and competitive species of *Uca* had no significant effect on numbers of burrows dug. When restricted to the relatively high *Salicornia-Distichlis* marsh, *U. pugnax* survived less well than *U. pugilator*.

Respiration rates for *U. pugnax* are higher underwater than in air (Teal, 1959), probably because of increased activity necessary to ventilate the gills.

At normal habitat temperatures, *U. pugnax* (=*rapax*) from Trinidad showed a higher metabolic rate than from localities in the United States (Tashian, 1956). Tashian found that there is a decrease in sensitivity to temperature change from southern to northern populations, along with an increase in tolerance to low temperature. Teal (1958) found that temperatures experienced in nature are not limiting factors in distribution of *U. pugnax* in Georgia, though high temperatures near a lethal level occur at times in summer. He (1959) concluded that among marsh crabs studied (see "remarks *U. minax*"), *U. pugnax* exhibits the most highly developed thermal acclimation, and its abundance on the marshes may be explained in part by its ability to regulate its metabolism over a wide range of temperature. Vernberg (1959) and Vernberg and Tashian (1959) reinforced this conclusion, showing that *U. pugnax* exhibits a marked tendency to demonstrate seasonal thermal acclimation. Brett (1960) showed that the daily oxygen-consumption cycle is considerably modified by locomotion of the crabs. Gray (1957) found gill area per gram of weight in *U. pugnax* to be lowest among the East Coast *Ucas*.

Crane (1943) observed hibernating *U. pugnax* in New Jersey, where the burrows were weathered open along the muddy banks of small creeks and could only have been submerged at spring tides. In March at air temperatures of 1.7° to 5.5° C., the immobile crabs were found from the burrow mouths to about 4 inches below the surface. Slight warming in the hand or in the sun elicited fairly rapid movement.

In another vein, Passano (1960) found an inverse correlation between temperature and pro-

ecdysis duration in *U. pugnax*. Surprisingly, at some temperature between 15° and 22° C. proecdysis fails to proceed normally, though these animals experience much lower temperatures throughout their range. It was suggested that the northern limits of the species are influenced by the inability of larvae to molt in cold water; hence, adults cannot appear there.

Crane (1943) gave a detailed description of the display and breeding relationships for this species. Display of males starts with the body elevated moderately high and both chelae held well off the ground and flexed in front of the mouth. Both chelipeds are extended obliquely upward, then the major claw is returned downward in a jerk or a series of jerks with no pause between extension and flexion. The fingers usually remain nearly closed, and a complete cycle of movement usually requires about 2 seconds. (Movement of the small chela is not described.) At times males will exhibit a series of bobbings or "curtseys," especially when displaying to females. Pearse (1914) and others considered these activities to be courtship display.

Other activities which have received much attention in experiments are rhythmic cycles. Brown and his coworkers (Brown and Sandeen, 1948; Brown and Webb, 1948, 1949; Brown, Webb, Bennett, and Sandeen, 1954) showed that fiddler crabs (among them *U. pugnax*) exhibit temperature-independent, diurnal, rhythmical color changes. These rhythms may be altered, or delayed, by lowering temperature for a time, or by altering the period or time of illumination. They further demonstrated that possibly two centers of rhythmicity exist in these crabs, each capable of having its rhythm altered independently of the other, and with one center influencing the other. Brown, Fingerman, Sandeen, and Webb (1953) demonstrated that amplitude of diurnal cycles under constant conditions increased to a maximum in 2 weeks. Superimposed on diurnal cycles are tidal rhythms which persist in phase with native local conditions under constant laboratory conditions. Oxygen consumption reflects these cycles as well as a lunar cycle (Brown, Bennett, and Webb, 1954; Brown, Fingerman, and Hines, 1954; Brown, Webb, Bennett, and Sandeen, 1955). Bennett, Shriner, and Brown (1957) found that degree of spontaneous locomotor activity is also related to tidal cycles although the rhythm persists only about a week under constant conditions.

Primarily because of the tremendous asymmetry in chelipeds of male fiddler crabs, *Uca* became an object of studies on relative growth. (In some of these papers no clear species designation was made.) In fiddler crabs [*Uca pugnax*] the percentage weight of the chela alters throughout life from 2 percent (the value retained by the female) to 65 percent (Huxley, 1927). In the related larger species, *U. minax*, since allometric growth continues longer, the chela may weigh over three-fourths of the remainder of the body (77 percent). Increasing relative size of the chela is associated with an increasing asymmetry of the central nervous system. Thus, such animals have no fixed form, for the proportions of parts are changing throughout postlarval life. On this basis, Huxley challenged Morgan's (1923) statement that females with intermediate width abdomens (subject also to allometric growth, Huxley, 1924) were actually intersexual female types. Tazelaar (1933) explored the subtleties of relative growth in *U. pugnax* in detail, finding that walking legs near the great chela and near the wide abdomen of females also reflect relative growth influences.

Uca pugilator (Bosc, [1801 or 1802]). Sand fiddler

Figures 209C; 210 C, D; 211

Ocypoda pugilator Bosc, [1801 or 1802], p. 197.
Uca pugilator: Rathbun, 1918b, p. 400, pl. 141; pl. 160, fig. 2 (rev.).—Hay and Shore, 1918, p. 452, pl. 37, fig. 2.

Recognition characters.—Carapace subquadrilateral, up to 1.5 times as wide as long, widest behind outer orbital angles, very convex, smooth; a shallow H-shaped depression near center of carapace and a narrow, flattened shelf behind orbit. Lateral margin strongly curved outward behind orbit, continued backward and inward as a low, well-defined ridge across entire frontoorbital width. Front more than one-third of frontoorbital width, broadly rounded below. Orbits large, open, upper margin slightly sinuous, lower margin dentate. Eyestalks long, slender. Antennule and antenna small. Merus of second maxilliped with 150 to 200 spoon-tipped hairs arranged in about 10 rows on inner side.

Chelipeds in male very unequal, in females equal and small. Merus of large chela with short,

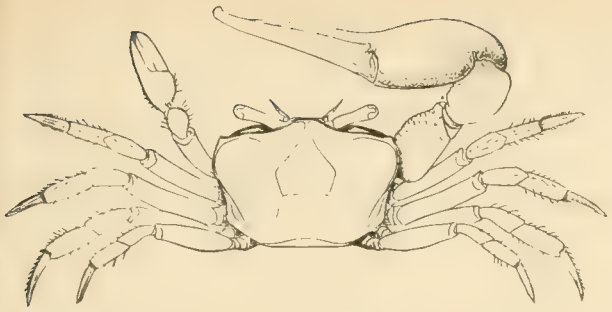

FIGURE 211.—*Uca pugilator* (Bosc). Male in dorsal view, about natural size (after Rathbun, 1884).

granulated, rugose lines above and with isolated dark hairs proximally, nearly smooth outside, lower margins granulate; merus of small chelipeds with scattered hairs. Carpus and outer surface of large hand with tubercles diminishing to granules on lower face of hand. Inner surface of palm without oblique tuberculate ridge as in *U. minax* and *U. pugnax*, but with a tuberculate ridge running along immovable finger from tip backward on internal distal border; surface granulate, granules coarser on thickest part of palm. Fingers strong, gaping; immovable finger with largest tubercles just behind middle and near truncate tip, inferior surface convex; dactyl evenly denticulate and with irregularly placed large tubercles, strongly curving downward past tip of opposed finger. Walking legs narrow.

Measurements.—Carapace: male, length, 17 mm.; width, 26 mm.

Color.—Carapace of male a dull light purplish or grayish blue of varying shades, or with irregular markings of brown or dark gray, a large patch of deep purplish blue on anterior half; large cheliped dull light blue at base with white tubercles, articulations yellowish; fingers mostly white; small chelipeds and legs buff with blue or brown speckles (various authors). Specimens from Massachusetts, bluish gray; those from Florida, reddish yellow (Démeusy, 1957).

Habitat.—This species occurs in countless numbers on sandy and muddy beaches bordering marshes, and along banks of tidal creeks. The crabs also occur farther from water in sandy situations of the *Salicornia-Distichlis* marsh and at times in *Juncus* marsh where the soil is sandy (Teal, 1958). The species burrows much as does *U. pugnax*, and populations of the two species are often intermingled (Pearse, 1914), though *U. pugilator* prefers sandier situations (Hyman, 1922). Dembowski (1926) found that choice of a place to burrow depends upon many factors, among them phototaxis and thigmotaxis. Burrows may have any shape but are unbranched and usually dug at an angle to the surface of the ground, the length of the burrow depending in part on the amount of moisture in the ground. Digging by males is done with legs on the side opposite the large claw. The crabs plug the opening as soon as they feel the water level rising in the burrow with the tide, and do this by pulling in the edges of the burrow and by ramming sand up from below. The end chamber, thus, functions as an air chamber during high tide.

Type locality.—"Caroline."

Known range.—Boston Harbor, Mass., to Texas; Old Providence Island (Coventry, 1944); Haiti.

Remarks.—*Uca pugilator*, like its east American congeners, has been the subject of much study, and one of the most readable accounts of its natural history is that of Hyman (1922).

In the vicinity of Beaufort, N.C., ovigerous females are found in spring and early summer. In Virginia, they are known from March to July (U.S. National Museum records). Schwartz and Safir (1915) found ovigerous females at Long Island, New York, from the first week in July until mid-August; in Massachusetts, Pearse (1914) found no ovigerous specimens until the first part of August. In Texas, Hedgpeth (1950) reported zoeae taken in a plankton net on May 20 at Long Lake. The breeding season, thus, is similar to those of the species discussed above in being seasonally related to latitude. Schwartz and Safir (1915) and Hyman (1920, 1922) stated that ovigerous females were rarely seen at the surface, but Hyman found that they left their burrows to aerate the eggs in water for a time at dusk. When the eggs were ready to hatch, the zoeae were released at such time in the water.

The larval and postlarval stages of the East Coast species of *Uca* were described and illustrated by Hyman (1920) based largely on study of *U. pugilator*. Hyman could find no consistent morphological differences among each stage of the three species. Five zoeal stages and a megalops stage were described. Gray (1942) described a

transitory prezoeal stage. Hyman found the first two zoeal stages most abundant at the surface, the third probably at intermediate depths, and the fourth and fifth zoeae usually on the bottom. He found the zoeal stages to last collectively about a month.

The megalops, a single stage lasting nearly a month, is a powerful swimmer. At the end of this stage the animal retires to cover of some sort, molts through two relatively weak crab stages and at last emerges as an active small crab measuring about 2 mm. across the carapace.

Feeding movements in *U. pugilator* are essentially the same as in the other two species of *Uca* and are discussed in the account for *U. pugnax*. Schwartz and Safir (1915) found the males moved the small cheliped to the mouth 28 to 46 times per minute, and females 61 to 92 times, when actively feeding on small particles in sand. Teal (1958) found that this species may wander into tide pools and shallow creeks to feed underwater at low tide. Miller (1961) considered *U. pugilator* to be the most specialized in mouth parts among Carolinian *Ucas* and well adapted to feeding on coarse substrate such as protected sandy beaches.

In experiments on salinity tolerance, Teal (1958) found that in fresh water 50 percent of *U. pugilator* died after 3.5 days. In water of 7 °/₀₀ more than 50 percent of the animals survived a 10-day test. Given a choice of fresh or 30 °/₀₀ sea water, *U. pugilator* chose salt water, but preferences shown by females were less strong than those shown by males, as was true also of *U. pugnax*. Teal concluded that this species lies between *U. minax* and *U. pugnax* in its tolerance of fresh water and can survive soakings of the *Salicornia* marsh with rain between spring tides.

Given a choice of sand or mud substrate above or underwater, *U. pugilator* burrowed almost exclusively in sand above water level. When either of the other species of *Uca* was present as a competitor for space, there was a reduction of 50 percent in the number of burrows that *U. pugilator* dug in sand above water. In tanks where there was no favorable substratum of sand above water, its behavior was not changed by presence of another species. When restricted to an unfavorable, low, muddy marsh, *U. pugilator* did not survive. Teal conjectured that this species cannot feed properly where sand is absent.

Respiration rates for this species are higher underwater than in air (Teal, 1959), probably due to increased activity necessary to ventilate the gills.

Teal (1958) found that temperatures of 45° C. on open sand flats of the *Salicornia-Distichlis* marsh in Georgia prevent *U. pugilator* from permanently occupying these areas, though they do feed there in cooler parts of the year. In general, temperatures experienced in nature were not considered a limiting factor. Orr (1955) found that *U. pugilator* died in 81 minutes at 40° C., in 18 minutes at 41° C., in 9 minutes at 43° C.. and in a little less than 9 minutes at 46° C. Démeusy (1957), investigating respiratory rates in populations of this species from Florida and Massachusetts, found that the northern population had a higher rate of metabolism at low temperatures (1.4° C.) than the Florida population, but that at 15° C. the difference was not significant. Démeusy found the northern population less sensitive to temperature change and more resistant to low temperature than the Florida population. On the other hand, Edwards (1950) found metabolic differences in these populations at 20° C. Teal (1959) found that above 25° C. specimens from Georgia showed no adjustment of respiration for temperature acclimation, but that below 20° C. there was some evidence of acclimation though not so well developed as in *U. pugnax*. Vernberg (1959) pointed out that metabolic activity in *Uca* of the temperate zone exhibits a seasonal cycle and that this cyclic change must be taken into account in comparing physiologic activity of relatives at different latitudes. Moreover, he stated that metabolic response of fiddler crabs has real significance in their distribution.

Crane (1943) gave a detailed description of the display and breeding relationships for this species. Display of males starts with the body elevated, cheliped tips lowered, and the meral-carpal joint of the major cheliped elevated. The cheliped is then extended up and out, the crab at the same time raising to tiptoe. The cheliped is held out for an instant, then smoothly returned to the original position. The minor chela makes weak corresponding gestures and fingers of both chelae are nearly closed throughout. Waves are made at a rate of about one per second. At moments of

extreme excitement, the major cheliped may be rapped against the ground in a flexed position.

Burkenroad (1947b) observed a drumming sound produced by males vibrating their large cheliped just outside the burrow at night, or in daytime just after waving and retreating into the burrow. Pearse (1914) was never able to observe copulation in the field following display, but did observe five matings of captive pairs in the laboratory. Females mated in the "hard shell" condition.

Color changes in *U. pugilator* have been investigated extensively in recent years. Carlson (1937) contended that the chromatophores respond to humoral control by the sinus gland in the eyestalks. Brown and Sandeen (1948) and Brown and Webb (1948) showed that there is a rhythmic secretion of hormone which operates to disperse the black and white pigments in the day and concentrate these at night. Superimposed on these responses are responses to background color, to total illumination, and to temperature, such that both pigments tend to disperse as intensity of illumination increases; but black pigment tends to concentrate as temperature increases above or decreases below about 15° C., and white pigment tends to disperse as temperature is increased above or decreased below about 20° C. Such lightening or darkening has been recorded in the field by a number of observers. Brown (1950) extended Carlson's work on red chromatophores, giving evidence for the activating principles and their daily rhythmicity. Further experiments with black chromatophores (Webb, Bennett, and Brown, 1954) showed that the diurnal rhythmic darkening and lightening are independent of structures in the eyestalks and that a substance which concentrates black pigment participates in regulation of the chromatophore system. Guyselman (1953) described a series of five color changes or stages which occur during the premolt period of normal animals. He found (as suggested earlier by Abramowitz and Abramowitz, 1940) that the sinus gland-X organ complex plays a role in regulation of metabolism of water and inorganic constituents. Evidence of a diurnal rhythm of water uptake was presented. Fingerman (1956) showed that even in the Gulf of Mexico, where tides are daily, the persistent rhythmic color changes remain scheduled as they are in crabs living where tides are semidiurnal, but (1957) that for a given local area the phase may be slightly altered according to the time that the burrows are uncovered by a receding tide.

Extending their investigations on rhythmicity, Brown, Webb, Bennett, and Sandeen (1955) showed that oxygen consumption in both *U. pugilator* and *U. pugnax* shows apparent persistent trends related to solar and lunar cycles.

As a sidelight to work with eyestalkless *U. pugilator*, Brown and Jones (1949) found that removal of eyestalks from adult females resulted in a period of rapid ovarian growth, with accompanying increase in oocyte diameter and a color change of the ovary from light pink to deep purple. Eggs produced by such animals failed to become attached to the pleopods.

The subject of intersexuality and relative growth was reopened by Darby (1935) as a result of examination of some 9,000 specimens of *U. pugilator* collected at Beaufort, N.C. Among these, 12 females were obtained with 2 fiddles, but no female was found in 1 large chela. These 12 specimens had fully widened, typically female abdomens and were always found feeding with the males in contrast to the other small-clawed females which stayed close to their holes. Darby termed these female-to-male intersexes. A male-to-female intersex; that is, a crab with a typical male abdomen and normal reproductive appendages, yet with small claws, was found only once, at Charleston, S.C. Because feeding is accomplished with the small claw, even partially symmetrical males must be handicapped in obtaining food, and it is not surprising that perfectly symmetrical adults do not, or rarely, occur. Darby, thus, refuted the arguments of Huxley and Rathbun that females with narrow abdomens were merely extremes in the normal variation curve for female abdomen growth, and supported the contention of Morgan that these were truly intersexes.

Superfamily **Oxyrhyncha**

Carapace more or less narrowed in front, and usually produced to form a rostrum; branchial regions considerably developed, hepatic regions small. Epistome usually large; buccal cavity quadrate, with anterior margin usually straight.

Gills almost always nine in number on each side; efferent channels opening at sides of endostome or palate. Antennules longitudinally folded (Rathbun, 1925).

Family **Majidae**

Chelipeds specially mobile, usually about same size as other legs with fingers straight. Second article of antenna well developed, generally fused with epistome and often with front. Orbits generally more or less incomplete. Hooked hairs almost always present. Male openings coxal (Borradaile, 1907). Palp of external maxilliped articulated either at summit or at anterointernal angle of merus (Alcock, 1895). First pleopod greatly exceeding second pleopod in length (Garth, 1958).

KEY TO SUBFAMILIES OF MAJIDAE IN THE CAROLINAS

Modified after Garth (1958)

a. Eyes either without orbits, or with commencing orbits.
  b. Eyes without orbits; eyestalks generally long, either nonretractile, or retractile against sides of carapace, or against acute postocular spine affording no concealment; basal (fused) antennal article extremely slender and usually long---------*Inachinae* (p. 236).
  bb. Eyes with commencing orbits; basal (fused) antennal article not extremely slender.
    c. Eyes lacking a postocular cup, but with tubelike housing.
      d. Eyestalks long; orbit partially protected by a hornlike supraocular spine or eave, a strong postocular tooth, or both; body truncate in front *Ophthalmiinae* (p. 246).
      dd. Eyestalks short, relatively immobile, and either concealed by a supraocular spine, or sunk in sides of rostrum; basal antennal article truncate-triangular----- *Acanthonychinae* (p. 248).
    cc. Eyes with cupped postocular process into which eye retracts, and with a supraocular eave or spine *Pisinae* (p. 250).
aa. Eyes with complete or nearly complete orbits; basal antennal article broad, expanded to form floor to orbit *Mithracinae* (p. 254).

Subfamily **Inachinae**

Eyes without orbits; eyestalks generally long, either nonretractile, or retractile against sides of carapace, or against an acute postocular spine. Basal article of antenna extremely slender throughout its extent, and unusually long (Alcock, 1895). First pleopod not very stout, straight or curved, apically tapering, but apex most varying (hairy, spinose, naked, etc.; acute, blunt, bifid, etc.); second pleopod short (Stephensen, 1945).

KEY TO GENERA OF INACHINAE IN THE CAROLINAS

Modified after Garth (1958)

a. Seven free abdominal segments in both sexes; rostrum double----------*Anomalothir* (p. 236).
aa. Six free abdominal segments in male, five in female.
  b. Rostrum double.
    c. Interantennular spine present and conspicuous.
      d. Spine of basal antennal article equally advanced with front----------*Euprognatha* (p. 237).
      dd. Spine of basal antennal article not equally advanced with front-------*Batrachonotus* (p. 238).
    cc. Interantennular spine absent or inconspicuous. *Collodes* (p. 239).
  bb. Rostrum single.
    c. Merus of outer maxilliped as broad as ischium; palp of moderate size.
      d. Postorbital tooth large, curving around side of eye----------*Pyromaia* (p. 240).
      dd. Postorbital tooth small, or if large not curving around side of eye----------*Anasimus* (p. 240).
    cc. Merus of outer maxilliped often narrower than ischium; palp large and coarse.
      d. Rostrum considerably less than postrostral length; basal antennal article often longitudinally sulcate----------*Podochela* (p. 241).
      dd. Rostrum approaching or surpassing postrostral length; basal antennal article not longitudinally sulcate.
        e. Carapace nodulose; a long spine at end of merus of walking legs; rostrum sparsely spined *Metoporhaphis* (p. 243).
        ee. Carapace smooth; spine at end of merus of walking legs no longer than others; rostrum multispinose----------*Stenorynchus* (p. 244).

Genus ***Anomalothir*** Miers, 1879

Rathbun, 1925, p. 23.

Anomalothir furcillatus (Stimpson)

Figures 212, 223A

Anomalopus furcillatus Stimpson, 1871a, p. 125.
Anomalothir furcillatus: Rathbun, 1925, p. 24, text-fig. 6, pl. 8, fig. 2; pl. 9, fig. 2; pl. 206 (rev.).

Recognition characters.—Carapace much elongated, almost subcylindrical, pubescent, with regularly placed tubercles. Rostrum long, from two-thirds to 1.25 times as long as remainder of carapace, bifurcate, horns contiguous for half or more of length, slightly divergent. Eyes without orbits; pre- and post-orbital spines small, acute. Antenna visible in dorsal view, basal article narrow. Merus of maxilliped without notch at inner angle where palp inserts.

Chelipeds in adults longer than carapace; merus subcylindrical, with row of small spines below

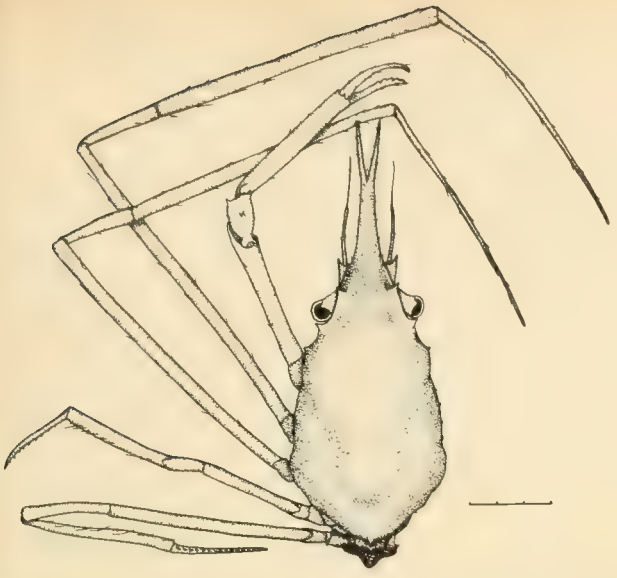

FIGURE 212.—*Anomalothir furcillatus* (Stimpson). Female in dorsal view, legs of right side not shown, 3 mm. indicated.

and less distinct row above; carpus with three spines on outer surface; palm unarmed, elongate; fingers short, stout, less gaping in male than in female. Walking legs pubescent; first two pairs long, slender; third and fourth pairs shorter, prehensile, with dactyls spinose on inner border; third pair shortest, merus with three strong hooked spines beneath, propodus and curved dactyl of about equal length; fourth pair intermediate in length, nearly straight, with propodus longer than dactyl.

Abdomen of both sexes with seven free segments.

Measurements.—Carapace: male, length including rostrum, 17 mm.; width, 6 mm. Length of rostrum, 7.5 mm. Carapace: female, length including rostrum, 20 mm.; width, 5 mm. Length of rostrum, 6 mm.

Color.—Light orange yellow; palms much deeper color (Henderson *in* Rathbun, 1925).

Habitat.—Rathbun (1925) listed this form from sandy, broken shell, pebbled, and rocky bottoms; 30 to 262 fathoms.

Type locality.—Off "The Samboes" [Southern Florida], 123 fathoms.

Known range.—Off Cape Lookout, N.C., through Gulf of Mexico and West Indies to Grenada.

Remarks.—Though the depth range of this species is usually beyond the 100-fathom mark, it may occur in shallower water in the Carolinas. Ovigerous females are known from the northeastern Gulf of Mexico in March.

Genus ***Euprognatha*** Stimpson, 1871

Rathbun, 1925, p. 95.

Euprognatha rastellifera marthae Rathbun

Figures 213, 223B

Euprognatha rastellifera Stimpson, 1871a, p. 123.—Hay and Shore, 1918, p. 454, pl. 37, fig. 7.

Euprognatha rastellifera marthae Rathbun, 1925, p. 96, text-fig. 30, pl. 33; pl. 34, figs. 1–2; pl. 35, figs. 3–4; pl. 216 (rev.).

Recognition characters.—Carapace pyriform, granulate, a tubercle or short truncate spine on gastric and cardiac regions, each branchial region, and supraorbital margin. Rostrum short, with two small teeth on horns. Ocular peduncles short, with tubercle at emargination of cornea. Frontal teeth short, spiniform, or triangular. Postorbital projection dentiform, triangular, tapering to a slender point. Obtuse antennal spines directed obliquely forward, approximately as advanced as front; interantennular spine inclined downward, equaling or surpassing front. Sides of hepatic and pterygostomian region with a few

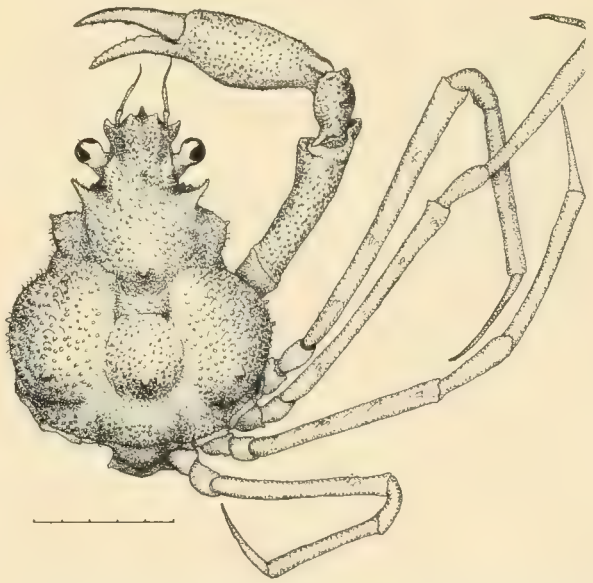

FIGURE 213.—*Euprognatha rastellifera marthae* Rathbun. Male in dorsal view, legs of left side not shown, 5 mm. indicated.

small spines. Sternum granulate except for concave portion between chelipeds.

Chelipeds approximately twice as long as carapace, granulate, margins spinous; hand swollen; fingers more than half length of palm, slightly gaping. Walking legs granulate, with tufts of curled setae and often small spines; first pair longest, others successively shorter.

Abdomen of males with six, females with five, free segments.

Measurements.—Carapace: male, length, 14 mm.; width, 12 mm.

Variations.—Rathbun (1925) divided the species *E. rastellifera* into a northern subspecies, *marthae* (ranging from Nantucket to southern Florida), and a southern or Caribbean subspecies, *acuta* (ranging from Cuba to Grenada and Barbados), with a region of intergradation in the Florida Keys from which *rastellifera* was originally described. The southern subspecies (*acuta*) has longer, sharper, and more slender spines than *marthae*, and a narrower, higher, and more closely and finely roughened carapace with regions more deeply separated than in the more northern forms. Likewise, the chelipeds have spines on the border of the merus well developed and legs more spinulose than in the northern forms.

Rathbun pointed out that there is considerable overlap in distribution of these subspecies, listing *acuta* from as far north as Marthas Vineyard. Such subspecific treatment seems untenable today, for such overlap of geographic range can hardly exist. No typical form was designated. I have retained the subspecific name *marthae* for the Carolinian form simply because this region lies well within the range mentioned by Rathbun, but I have not studied all of the material comparatively.

Habitat.—The species has been reported from a variety of sandy and muddy bottoms; 44 to 217 fathoms.

Type locality.—Southwest of Marthas Vineyard, Mass., lat. 40° N. long. 70°57′ W., 85 fathoms.

Known range.—Off Georges Bank (lat. 40°35′ N. long. 67°37′ W.) to Carysfort, Fla.

Remarks.—Rathbun (1925) reported an ovigerous female off Marthas Vineyard in July, and they are known off Georges Bank in November (U.S. National Museum records).

Genus *Batrachonotus* Stimpson, 1871

Rathbun, 1925, p. 122.

Batrachonotus fragosus Stimpson

Figures 214, 223C

Batrachonotus fragosus Stimpson, 1871a, p. 122.—Rathbun, 1925, p. 123, text-fig. 48, pl. 39, figs. 1–4 (rev.).

Recognition characters.—Male. Carapace triangular, broadly expanded behind; gastric, cardiac, and branchial regions strongly protuberant, each surmounted by a stout spine or large tubercle; intestinal region with two small tubercles just above posterior margin; hepatic region angular, approximating postorbital tooth. Cervical depressions deep and broad giving carapace superior outline much like frog's back. Rostrum short, formed of rounded lobes separated by a shallow notch, scarcely projecting beyond antennulary fossae, margin and supraorbital margin denticulate. Basal articles of antenna with dentate margins and a small tooth at anterior extremity. Merus of outer maxilliped broad with prominent outer and inner anterior angles. Abdomen and sternum granulate except for smooth area be-

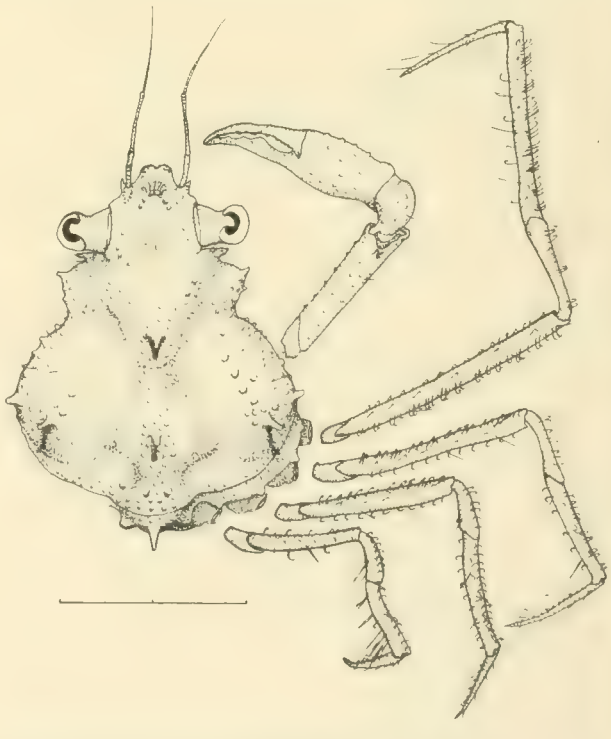

FIGURE 214.—*Batrachonotus fragosus* Stimpson. Animal in dorsal view, legs of right side shown in approximate position, legs of left side not shown. 2 mm. indicated.

tween chelipeds; abdomen with six free segments, last two fused, proximal fixed segment with a prominent median spine.

Chelipeds somewhat longer than carapace, spinulose; ischium with distal spine; hand slightly compressed; fingers nearly as long as palm, gaping nearly whole length, a large tooth in middle of immovable finger. First pair of walking legs more than twice length of second pair, posterior pairs short.

Female. Carapace narrower behind and wider in front than male, tuberculation more uniform, spines less frequent. First walking leg little longer than second, approximately 1.5 times length of carapace. Abdomen tuberculate or granulate, with five free segments, last three fused.

Measurements.—Carapace: male and female, length, 7 mm.; width, 6 mm.

Variations.—Rathbun (1925) stated that this species exhibits wide variations from the type. Some specimens have the elevated regions surmounted by a spine, some have an abdominal spine, others even lack tubercles on the elevated regions.

Habitat.—The species has been reported from mud, sand of various grades, and broken-coral and shell bottoms; shore to 75 fathoms.

Type locality.—South of Tortugas, [Fla.], lat. 24°36′40″ N. long. 80°02′20″ W., 16 fathoms.

Known range.—Cape Hatteras, N.C., to southern and western Florida; West Indies to Rio de Janeiro, Brazil. Ovigerous females are known from Tortugas in June (U.S. National Museum records).

Genus ***Collodes*** Stimpson, 1860

Rathbun, 1925, p. 105.

Collodes trispinosus Stimpson

Figures 215, 223D

Collodes trispinosus Stimpson, 1871a, p. 120.—Rathbun, 1925, p. 107, text-figs. 32a, b; pl. 36, figs. 5–6 (rev.).

Recognition characters.—Carapace ovate-triangular, covered with coarse granules except on front, anterior portion of gastric region, and about bases of spines; a single, slender, erect, capitate spine on gastric and cardiac regions, and on first abdominal segment. Rostrum short, with two minute and usually well-separated horns. Eyes of moderate length, partially retractile; postorbital tooth slender, a granule on upper orbital border. Antenna with first movable article approximately as long as rostral horns; basal article of antenna twisted, with four or five spinules on outer border and with a laminate crest on inner margin ending in a large tooth; interantennular spine short. Merus of outer maxilliped obcordate, deeply cut on distal margin, strongly produced at inner and outer angles.

FIGURE 215.—*Collodes trispinosus* Stimpson. Male in dorsal view, legs of left side not shown, 5 mm. indicated.

Chelipeds of male moderately stout, palm thick, smooth outside; surface of carpus and margins of merus and palm spinulose; fingers widely gaping, with a triangular tooth near middle of immovable finger and a low molariform tooth near base of dactyl. Walking legs long; first two pairs variably subequal; third and fourth pairs successively shorter; dactyls as long as propodi.

Measurements.—Carapace: male, length, 14 mm., width, 12 mm.; female, length, 12 mm., width, 10 mm.

Habitat.—Rathbun (1925) reported this species from gray sands of varying coarseness, broken shell, and gravel bottoms; 4 to 82 fathoms.

Type localities.—Off the Quicksands, Carysfort Reef, and French Reef, [Fla.], 34 to 50 fathoms.

Known range.—Near Cape Hatteras, N.C., to south and west Florida near Apalachicola.

Remarks.—Rathbun (1925) reported ovigerous females from North Carolina in October, and they are known from Florida in July (U.S. National Museum records).

Genus *Pyromaia* Stimpson, 1871

Rathbun, 1925, p. 127.

Pyromaia cuspidata Stimpson

Figures 216, 223E

Pyromaia cuspidata Stimpson, 1871a, p. 110.—Hay and Shore, 1918, p. 455, pl. 38, fig. 4.—Rathbun, 1925, p. 129, text-fig. 49; pl. 41 (rev.).

Recognition characters.—Adult male. Carapace pyriform, approximately two-thirds as wide as long; regions well marked, tumid, rough, with scattered granules, sharp tubercles and spines; often six large median spines (two mesogastric, one urogastric, two cardiac, one intestinal), elsewhere one protogastric, two or three hepatic, remainder branchial. Depressions separating branchial regions from other regions somewhat pitted. Rostrum tapering to a point, trigonal; upper and lateral margins spinulose. Interantennular spine acute, triangular, pointing downward and forward. Orbits large, open; supraorbital spine almost erect, directed slightly outward and forward; postorbital tooth large, curved around end of eye; anterior margin fringed with hair. Basal article of antenna long, with terminal spine, a larger spine at middle of inner margin and a small one at middle of outer margin followed by row of tubercles or spinules. A tubercle at angle of buccal cavity. Outer maxilliped spinulose, a longitudinal depression on ischium, merus cordate.

Limbs covered with short fur, surface underneath roughened with sharp granules or spines; merus of cheliped armed on margins, terminal spine of upper margin longest; upper margin of carpus spinulose with a few spines on outer surface; hand inflated, fingers bare, grooved, slightly agape at base. Walking legs spinulose; meri with distal spine; first legs longest, remainder successively shorter.

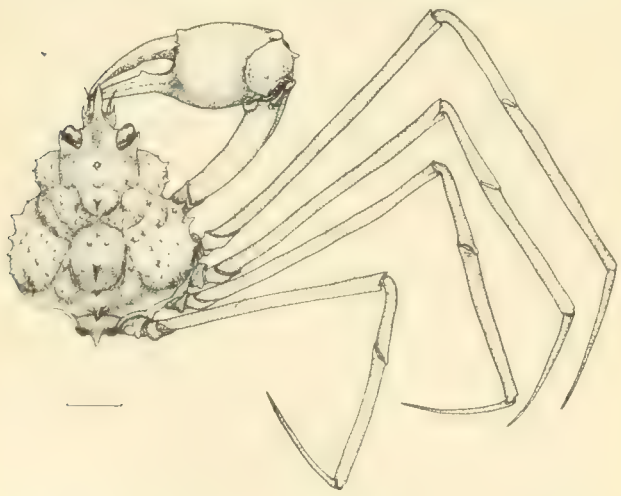

FIGURE 216.—*Pyromaia cuspidata* Stimpson. Male in dorsal view, legs of left side not shown, 10 mm. indicated.

First abdominal segment long, with an acute backward-pointing spine; six free segments, last two fused.

Adult female. Limbs almost bare; chelipeds not much stronger than walking legs, dactyl longer than palm; legs shorter than in male. Five free abdominal segments, last three fused.

Measurements.—Carapace: male, length, 41 mm.; width, 32 mm.

Variations.—The young have pubescence resembling that in females, the postorbital tooth smaller than in adults, slender and directed outward in small specimens (7.5 mm. long), directed outward and forward in somewhat larger forms.

Color.—Immature individuals brown, legs with lighter crossbands.

Habitat.—This species has been taken on gray mud, sand, pebble, and broken-coral bottoms; 15 to 300 fathoms.

Type localities.—Off Sand Key, 82 fathoms; Alligator Reef, 88 fathoms; the Samboes, 93 and 121 fathoms; southwest of Sand Key, 125 fathoms [Florida].

Known range.—Off Cape Lookout, N.C., to west Florida; Yucatan Channel; Cuba.

Remarks.—U.S. National Museum records show ovigerous females off Florida in February and July.

Genus *Anasimus* Milne Edwards, 1880

Rathbun, 1925, p. 64.

Anasimus latus Rathbun

Figures 217, 223F

Anasimus latus Rathbun, 1894, p. 58.—1925, p. 65, pl. 214 (rev.).

Recognition characters.—Carapace broadly ovate, elevated on median line, posterior half semicircular, anterior half broadly triangular, surface covered with unequal granules. Carapace with median row of spines, two gastric (posterior one larger), one large cardiac, one small backward-pointing intestinal, and a long acuminate backward-projecting spine at distal end of first

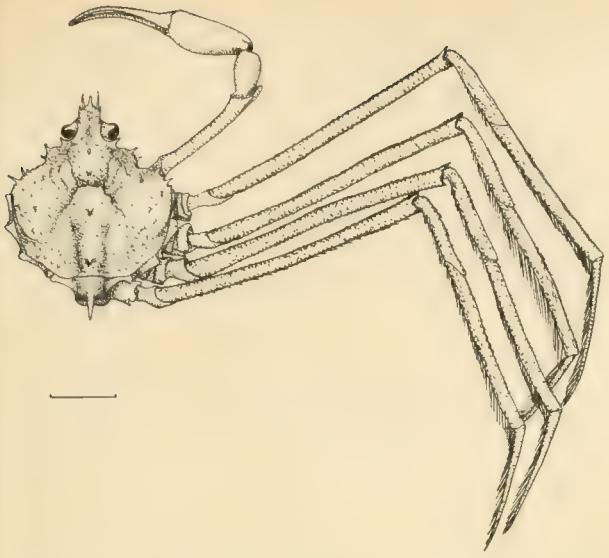

FIGURE 217.—*Anasimus latus* Rathbun. Male in dorsal view, legs of left side not shown, 10 mm. indicated.

abdominal segment; anterior gastric spine one of transverse row of about five; branchial region with three small spines or tubercles in triangular arrangement. Three anterolateral spines, one hepatic and two branchial above base of cheliped. Rostrum short, medially carinate, broadly triangular at base, ending in short, sharp, upturned spine. Eyes large; prominent supraorbital spines separated by depression, postorbital spines long, exceeding eye in large specimens. Antenna short, slightly exceeding rostrum, basal article with terminal spine and a stout spine pointing downward and forward in front of eye. Pterygostomian region with row of spines and spinules continued to antennal segment including long spine at angle of buccal cavity. Sternum of male coarsely granulate.

Chelipeds of male more than twice length of carapace, granulate; merus cylindrical; palm swollen, shorter than fingers; fingers slender, curved inward, gaping at base only, finely and evenly toothed except for larger basal tooth on dactyl. Female with chelipeds a little longer than carapace but smaller than in male, fingers not gaping. Walking legs long, slender, cylindrical, roughened, except on dactyl, with numerous short, stout, appressed spinules; propodi and dactyls with double fringe of hair.

Abdomen of male with six, female with five, free segments; female with median tubercle on third and fourth segments.

Measurements.—Carapace: male, length, 26 mm., width, 24 mm. Length of cheliped, 58 mm., of first walking leg, 106 mm.

Variations.—The adults are relatively broader than the young whose rostrum and dorsal spines are longer. The postorbital spines are very small, pointing directly outward, and with little more than a tubercle in specimens 9 mm. long or less.

Color.—Recently preserved specimens show dark reddish or brown rings on the legs (Holthuis, 1959).

Habitat.—This form has been taken from coarse sand, coral, coral sand, and mud and shell bottom; 26 to 88 fathoms.

Type locality.—Gulf of Mexico, east of Delta of Mississippi River, lat. 29°14′30″ N. long 88° 09′30″ W., 68 fathoms.

Known range.—Off Cape Lookout, N.C., to off Tabasco, Mexico (Hildebrand, 1954); west of Trinidad, and off Surinam (Holthuis, 1959).

Remarks.—Ovigerous females have been reported from southern Florida and the northern Gulf of Mexico in all seasons of the year, from North Carolina in June (Rathbun, 1925, and U.S. National Museum records), and Surinam from April to August (Holthuis, 1959).

Genus ***Podochela*** Stimpson, 1860

Rathbun, 1925, p. 31.

KEY TO SPECIES IN THE CAROLINAS

a. Rostrum broad, rounded in front.
  b. Dactyls of last three pairs of legs less than one-half length of propodus; pterygostomian region bearing a broad, spinelike projection ..... *riisei* (p. 241).
  bb. Dactyls of last three pairs of legs one-half or more length of propodus; pterygostomian region bearing a long thin lamina ..... *sidneyi* (p. 242).
aa. Rostrum long, spiniform ..... *gracilipes* (p. 243).

Podochela riisei Stimpson

Figures 218, 223G

Podochela riisei Stimpson, 1860a, p. 196, pl. 2, fig. 6.—Hay and Shore, 1918, p. 453, pl. 37, fig. 9.—Rathbun, 1925, p. 33, text-figs. 9a–b; pl. 11, figs. 1–2; pl. 208, fig. 2 (rev.).

Recognition characters.—Carapace pyriform, depressed, widest near posterior margin, greatest width about two-thirds length, dorsal region uneven and with tufts of hairs. Rostrum broad,

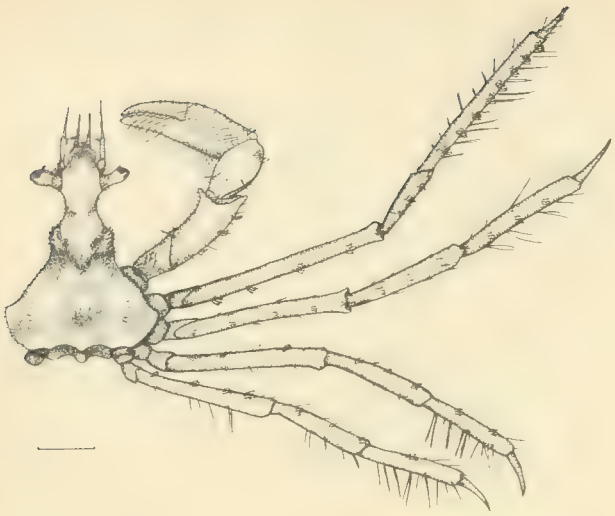

FIGURE 218.—*Podochela riisei* Stimpson. Animal in dorsal view, legs of left side not shown, 5 mm. indicated.

rounded in front, deeply excavated below for antennules, carinate above and with a tuft of curled hairs. Orbits rounded, margins thickened and with a row of hairs. Eyestalks short and stout, cornea oblique, dorsal emargination with distal tubercle tufted. Basal article of antenna with a high crest on each margin. Sternum of male thrown into ridges radiating to bases of legs.

Chelipeds slender in both sexes, fingers in contact throughout their length (stouter and slightly agape proximally in adult males). First pair of walking legs stouter than others, about three times as long as carapace; upper surface of all legs with regularly spaced tufts of stiff curled hairs.

Abdomen of male with six, female with five, free segments.

Measurements.—Carapace: male, length, 21 mm., width, 16 mm.; female, length, 23 mm., width, 20 mm.

Variations.—The rostrum is variable in shape and length. Margins of the basal antennal articles are thick in old individuals but may be thin in younger ones. Sternal segments of males usually have rounded surfaces but are sometimes flattened.

Color.—Overall color light brown; legs lighter, grading to almost off white or pale yellow; chelae and chelipeds nearly white to almost transparent; carapace darker on lateral aspects of urogastric and cardiac regions, as well as at posterolateral portions of metabranchial regions. Wass (1955) reported brick red specimens.

Habitat.—Has been taken from among hydroids on pilings at Beaufort, N.C., and in rocky areas in northwestern Florida (Wass, 1955); shallow water to 30 fathoms.

Type locality.—Island of St. Thomas, [West Indies].

Known range.—North Carolina to Campeche, Mexico; through West Indies to St. Thomas; Rio de Janeiro and south of Pernambuco, Brazil; Bermuda.

Remarks.—Ovigerous females have been taken in North Carolina in September. They have been taken in Florida from June to August and from November to February (U.S. National Museum records).

Podochela sidneyi Rathbun

Figures 219, 223H

Podochela sidneyi Rathbun, 1924, p. 1.—Rathbun, 1925, p. 39, text-fig. 9c, pls. 12–13 (rev.).

Recognition characters.—Closely resembling *Podochela riisei.* Rostrum narrower at base. Pterygostomian region bearing a long thin lamina either subtriangular or produced downward in a lobe. Sternal segments flat with sharp cristate margins.

Chelipeds of adult male less inflated than in *P. riisei*, proximal gape narrower, teeth on cutting edges more numerous and uniform in size. Walk-

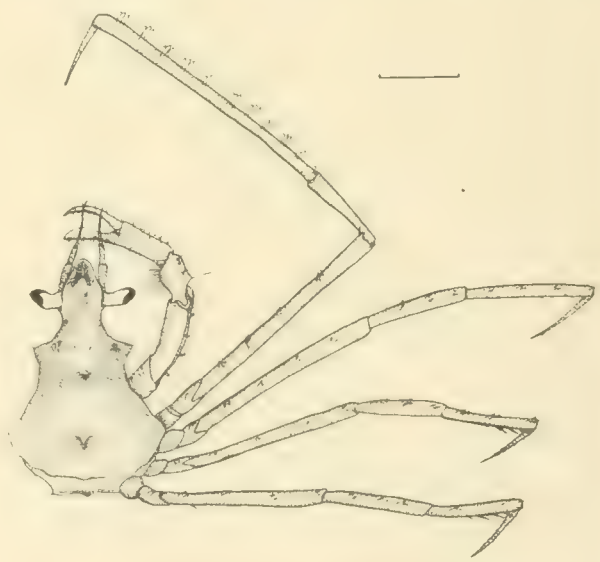

FIGURE 219.—*Podochela sidneyi* Rathbun. Animal in dorsal view, legs of left side not shown, 5 mm. indicated.

ing legs longer than in *P. riisei;* first pair of walking legs 3 or more times as long as carapace; dactyls of last three pairs less curved, longer and relatively more slender than in *P. riisei;* dactyl of second leg up to one-half length of propodus, of third leg to two-thirds, and of fourth leg to three-fourths length of propodus.

Abdomen of male with six, female with five, free segments.

Measurements.—Carapace: male holotype, length, 14 mm., width, 11 mm.

Habitat.—Shallow water to 102 fathoms.

Type locality.—Off Cape Hatteras, N.C., 49 fathoms.

Known range.—Off Cape Hatteras, N.C., to Port Aransas, Tex.; northwestern Cuba; Yucatan Channel.

Remarks.—Hildebrand (1954) reported the carapace of this species as decorated with hydroids and ascidians.

Podochela gracilipes Stimpson

Figures 220, 223I

Podochela gracilipes Stimpson, 1871a, p. 126.—Hay and Shore, 1918, p. 454, pl. 37, fig. 6.—Rathbun, 1925, p. 47, text-fig. 12, pl. 17 (rev.).

Recognition characters.—Carapace narrow, pyriform, depressed; constricted behind orbits; with rounded protuberance on cardiac region and two smaller median protuberances on gastric regions. Rostrum long, spiniform, hairy, unarmed. Sternum of males with thick blunt spine at base of cheliped. Crests on basal article of antenna less pronounced than in *P. riisei*, article long, narrow posteriorly, with a diagonal ventral ridge merging with terminal spine distally.

Chelipeds in male stout, inflated, fingers widely agape to near tip, large tooth near base of dactyl. Chelipeds slender in female. Walking legs slender, first pair three times length of carapace; dactyls long, nearly straight, one-third length of propodus; propodi of last three pairs thickened distally; dactyls slightly scythe-shaped, two-fifths length of propodus on second pair, one-half length on third, and two-thirds length of propodus on fourth pair.

Abdomen of male with six, female with five, free segments.

Measurements.—Carapace: male, length, 13 mm., width, 9 mm.; ovigerous females, length, 9 mm., width, 6 mm.

FIGURE 220.—*Podochela gracilipes* Stimpson. Animal in dorsal view, legs of left side not shown, 5 mm. indicated.

Habitat.—Eighteen to 120 fathoms.

Type localities.—West of Tortugas, off Pacific and Carysfort Reefs, [Fla.], 36 to 60 fathoms.

Known range.—Off Cape Lookout, N.C., to Gulf of Mexico; Caribbean Sea to Columbia and Barbados; Cabo Frio, Brazil.

Remarks.—Ovigerous females are known in December from North Carolina.

Genus ***Metoporhaphis*** Stimpson, 1860

Rathbun, 1925, p. 19.

Metoporhaphis calcarata (Say)

Figures 221, 223J

Leptopodia calcarata Say, 1818, p. 455.

Metoporhaphis calcaratus: Hay and Shore, 1918, p. 454, pl. 37, fig. 5.

Metoporhaphis calcarata: Rathbun, 1925, p. 21, text-fig. 5, pls. 6-7 (rev.).

Recognition characters.—Carapace triangular, longer than broad, uneven, nodulose with each nodule surmounted by a tubercle and this in turn usually with a pencil of soft, hooked hairs. Rostrum as long as or longer than carapace, subcylindrical, tapering to a point, often armed with four or five slender spines projecting outward alternately from opposite sides of lower surface, and with distal pair so close to tip as to give tip bi- or tri-spinose appearance. Eyes protuberant, peduncles terminating in superior spinule project-

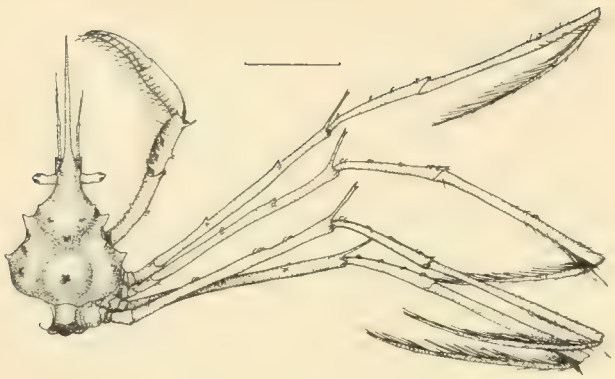

FIGURE 221.—*Metoporhaphis calcarata* (Say). Animal in dorsal view, legs of left side not shown, 10 mm. indicated.

ing beyond cornea. Basal antennal article with spine below at midpoint of length, another at outer distal angle, and a spinule at end of next two articles.

Chelipeds of moderate length, twisted, stout in male and less than half as long as first walking legs, margin of lower (really inner) surface armed with sharp spines; merus with sharp terminal spine; carpus with two sharp dorsal spines, one near each extremity of upper surface; hand broad, inflated; fingers about as long as palm, bent medially. Female with chelipeds feebler, palm shorter, fingers longer and more gaping. Walking legs slender, articles cylindrical but somewhat crooked; meri with one conspicuous spine and two smaller spines at extremity; dactyls longer than propodi, fringed with hair.

Male with six, female with five, free abdominal segments.

Measurements.—Carapace: female, length (including rostrum), 21 mm., width, 10 mm. Length of rostrum, 11 mm.

Color.—Dirty gray to lemon yellow.

Habitat.—Often found among hydroids near Morehead City, N.C., and also taken in dredges in Bogue Sound nearby; shallow water to 49 fathoms.

Type locality.—Bay of Charleston, S.C.

Known range.—Off Cape Hatteras, N.C., to Rio de Janeiro, Brazil.

Remarks.—Ovigerous females have been taken off South Carolina in August, and in Florida in March and August (Wass, 1955). Wass also noted that this species can remain suspended in water by "rhythmic waving of its long, setae-lined legs."

Genus *Stenorynchus* Lamarck, 1818

Rathbun, 1925, p. 13.

Stenorynchus seticornis (Herbst). Arrow crab

Figures 222, 223K

Cancer seticornis Herbst, 1788, p. 229, pl. 16, fig. 91 (see Rathbun, 1925).

Stenorynchus sagittarius: Hay and Shore, 1918, p. 455, pl. 37, fig. 8.

Stenorynchus seticornis: Rathbun, 1925, p. 13, text-fig. 3, pls. 2–3 (rev.).—Monod, 1956, p. 567, figs. 838–839.

Recognition characters.—Carapace smooth, triangular, longer than broad, diminishing in width to level of eyes and thence produced into a slender, horizontal, flattened, laterally spinuliferous rostrum varying from slightly longer to 2.5 times as long as carapace; rostral tip acuminate. Orbits not defined; postorbital spine small, occasionally bifid. Eyes short, not retractile. Basal article of antenna slender, with strong spine at middle directed downward and forward.

Legs extremely long and slender, composed of cylindrical articles, finely spinulose and bearing in addition two rows of spines on merus, two or three spines on carpus, and several terminal spines on these articles. Chelipeds slender, cylindrical; hand weak; palm of male cheliped from 2.5 to

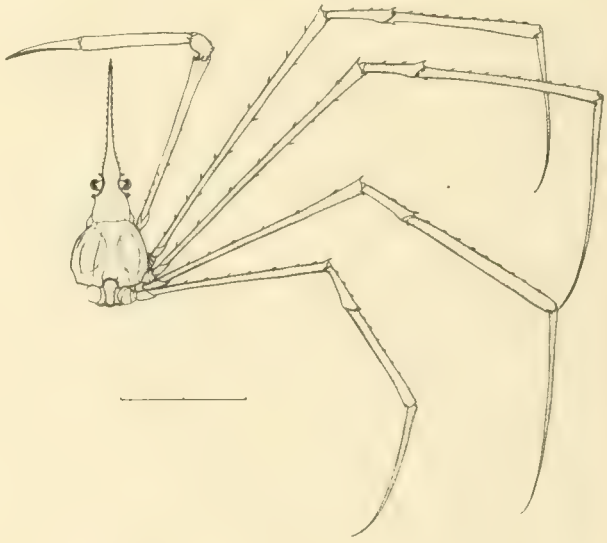

FIGURE 222.—*Stenorynchus seticornis* (Herbst). Animal in dorsal view, legs of left side not shown, 30 mm. indicated.

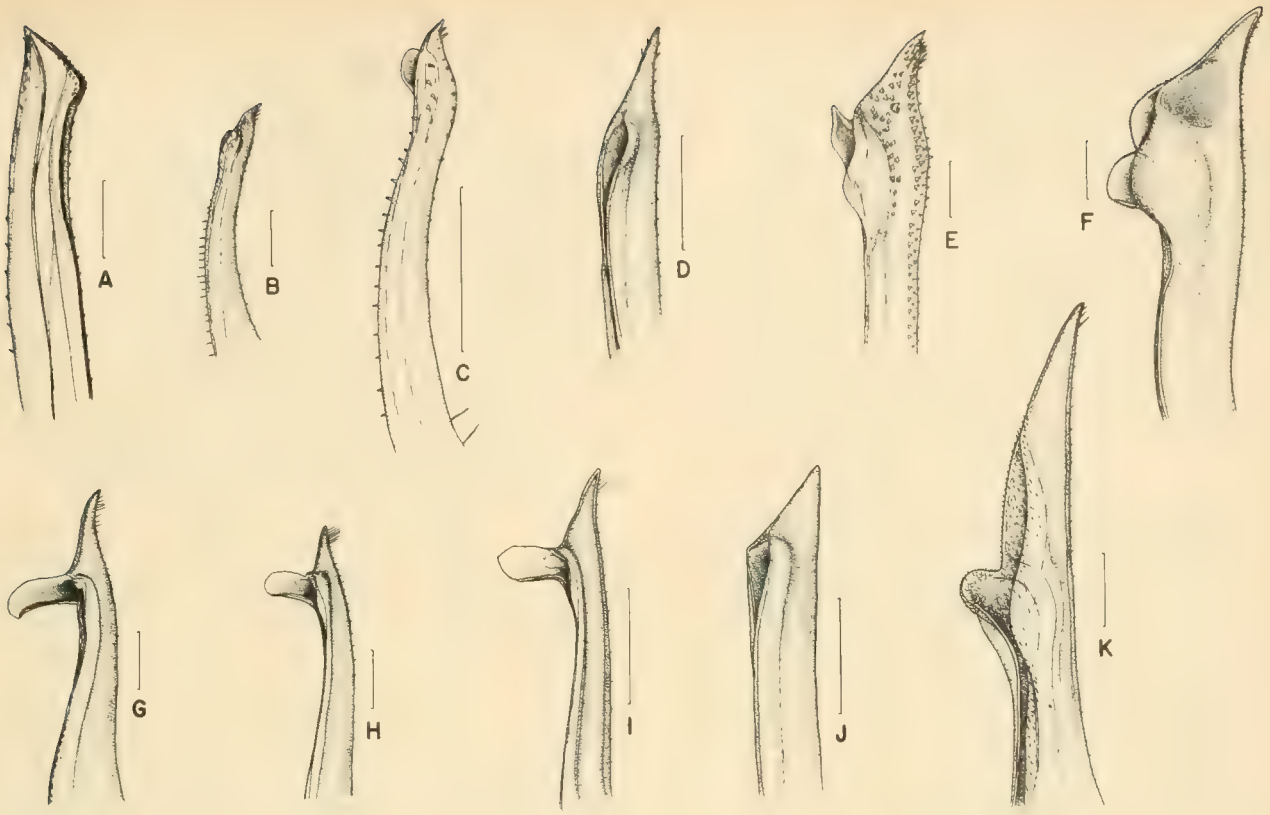

FIGURE 223.—Subfamily Inachinae, tips of right first pleopods of males; A, *Anomalothir furcillatus* (Stimpson), abdominal view; B, *Euprognatha rastellifera marthae* Rathbun, sternal view; C, *Batrachonotus fragosus* Stimpson, sternal view; D, *Collodes trispinosus* Stimpson, sternal view; E, *Pyromaia cuspidata* Stimpson, sternal view; F, *Anasimus latus* Rathbun, sternal view; G, *Podochela riisei* Stimpson, sternal view; H, *Podochela sidneyi* Rathbun, sternal view; I, *Podochela gracilipes* Stimpson, sternal view; J, *Metoporhaphis calcarata* (Say), sternal view; K, *Stenorynchus seticornis* (Herbst), sternal view; 0.33 mm. indicated.

4 times as long as dactyl. First pair of walking legs from 8 to 9 times as long as postrostral portion of carapace; second, third, and fourth legs successively shorter; dactyls on each pair longer than propodi.

Abdomen in male with six, female with five, free segments.

Measurements.—Carapace: male, length including rostrum, 57 mm.; width, 13 mm. Length of rostrum, 41 mm.

Variations.—There is great variation in length of rostrum, relative length of palm and fingers, and length of legs. In old individuals the rostrum, chelipeds, and legs are pubescent.

Color.—Body ground color gray, banded dorsally with stripes of light and dark brown or black converging anteriorly as a nested series of inverted V's; one dark pair of stripes continuing united on dorsal side and another more lateral pair of like color on ventral side of rostrum. Legs reddish brown, joints darker; fingers of chelipeds bluish purple.

Rathbun (1925) summarized other color observations. The general pattern is as above, with ground color creamy white, buff, or light orange vermilion; stripes white, chestnut, brown, or black; legs reddish with bright red spots at joints; chelae purple or mauve; spines on legs and rostrum orange or red; eyes maroon.

Habitat.—This form has been dredged or trawled from a variety of bottoms—rock, coral rock, pebbles, sand, or sand mixed with broken shell; also, it has been taken from wharf pilings and rock jetties. Near surface to 814 fathoms.

Type locality.—Guadeloupe (Holthuis, 1959).

Known range.—North Carolina to Rio de Janeiro, Brazil; Bermuda; eastern Atlantic from Madeira and Canary Islands to Angola.

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Remarks.—Though this species has a tremendous recorded range in depth, it is usually found well inside the 100-fathom mark. On September 6, 1953, an ovigerous female was collected from wharf pilings in Bogue Sound near Bogue Inlet, N.C.

Otherwise, ovigerous females are known or have been reported in the western Atlantic from February in the Gulf of Darien, throughout spring and summer in North and Middle America, and northern South America, to November off the Amazon River (U.S. National Museum records; Hildebrand, 1954; Holthuis, 1959; Rathbun, 1925).

Subfamily **Ophthalmiinae**

Orbit consisting, if complete, of a supraocular eave and a postocular spine; intercalated spine lacking . . . [but] . . . longer spinous outgrowths on supraocular eave and on postocular spine for most part present. Shape of body elongate, somewhat truncate in front, often provided behind with a median spine or outgrowth (Balss, 1929).

KEY TO GENERA OF OPHTHALMIINAE IN THE CAROLINAS

Modified after Garth (1958)

a. Eyes furnished with projecting and tubular commencing orbits ..... *Pitho* (p. 246).

aa. Orbit completely unprotected below; eyes protected above by a lamellate projection consisting of supraocular eave and an outgrowth of hepatic region ..... *Tyche* (p. 247).

Genus *Pitho* Bell, 1835

Garth, 1958, p. 162.

Pitho lherminieri (Schramm)

Figures 224, 233A

Othonia lherminieri Schramm, *in* Desbonne and Schramm, 1867, p. 20.

Pitho lherminieri: Hay and Shore, 1918, p. 459, pl. 38, fig. 8.—Rathbun, 1925, p. 362, text-fig. 117b, pl. 128, figs. 1–2; pl. 129, figs. 1–2; pl. 252, fig. 2 (rev.).

Recognition characters.—Carapace as broad as long in adult males, longer than broad in other individuals, narrow behind in males, broader in females, roughened with tubercles of different sizes, and adorned with scattered hooked hairs. Frontal teeth forming rostrum more advanced than orbital angles. Anterolateral margins armed with five strong teeth, exclusive of postorbital tooth; first tooth largest, second and third subequal, fourth and fifth much smaller, second occasionally bilobed. Orbits small, tubular, deep. Antenna short, with stiff hairs on borders; basal article lamellate, forming floor of orbit; second article flat, short, and broad; third article smaller, flattened.

FIGURE 224.—*Pitho lherminieri* (Schramm). Male in dorsal view, legs of left side not shown, 5 mm. indicated.

Chelipeds of adult male from 1.5 times to nearly twice length of body; merus subcylindrical; carpus and hand more or less compressed and distinctly angled along margins; fingers of adult male hollowed into spoon shape, touching only at extremity. In female and young male, fingers short and weak, evenly dentate, with margins in contact.

Abdomen of both sexes with seven free segments.

Measurements.—Carapace: male, length, 26 mm., width, 24 mm.; female, length, 18 mm., width, 17 mm.

Variations.—In females and young males the carapace is more tuberculate than in old males, the lateral teeth are sharper, and the last two teeth are more prominent than in mature males.

Color.—Dirty brownish yellow (Desbonne *in* Rathbun, 1925).

Habitat.—This species has been found on a variety of bottoms including mud, sand, shell-sand, shell, rock and coral, and grass (Rathbun,

1925). One-half to 28 fathoms, rarely to 120 fathoms.

Type locality.—Guadeloupe, in cavities of the keys.

Known range.—Off Beaufort Inlet, N.C., to west Florida; Vera Cruz, Mexico; West Indies to Islet of São Sebastião, São Paulo, Brazil.

Remarks.—Ovigerous females are known from May to November in the Bahamas and Florida, and in December from Brazil (Rathbun, 1925, and U.S. National Museum records).

Genus *Tyche* Bell, 1835

Garth, 1958, p. 172.

Tyche emarginata White

Figures 225, 226, 233B

Tyche emarginata White, 1847a, p. 206.—Hay and Shore, 1918, p. 461, pl. 39, fig. 4.—Rathbun, 1925, p. 508, pl. 272; pl. 273, figs. 7–12 (rev.).—Garth, 1946, pp. 406–408, text-fig. 1.

Recognition characters.—Carapace oblong-oval, flattened, with lamellate expansions in front covering ocular peduncles, and another prolonged and bilobed behind, stout hooked hairs on rostrum and prominent elevations. Front wide, with four long horns, lateral horns forming anterior angles of orbit, divergent, longer and more elevated than median rostral horns. Ocular peduncles entirely uncovered below. Gastric region swollen, with three low tubercles, two anterior, and a third posterior and median; cardiac region depressed, with three small tubercles. Lateral borders straight and nearly parallel at hepatic regions, rounded at branchial regions. Dorsal surface of hepatic region concave; branchial region with large tubercle on anterior lobe, and a prominent tuberculate crest above lateral margin. Exopodite of third maxilliped with basal protuberance recurving to cover base of ischium, merus inserting deeply into outer distal portion of ischium by similar but less developed process, inner margin of ischium strongly dentate.

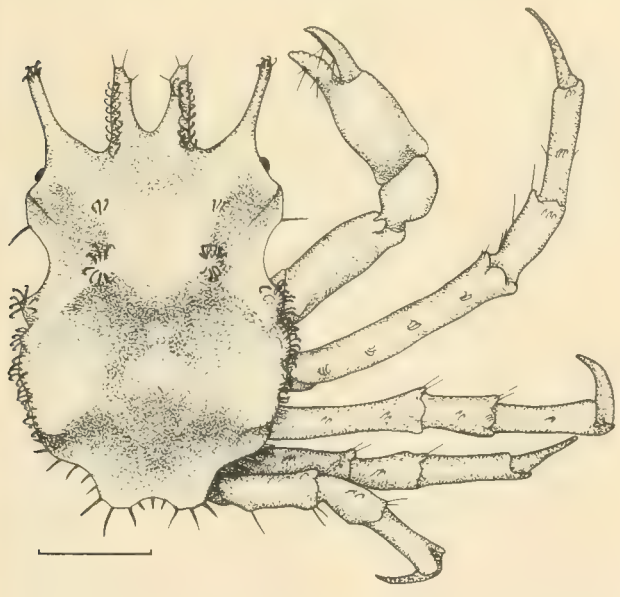

FIGURE 225.—*Tyche emarginata* White. Male in dorsal view, legs of left side not shown, 5 mm. indicated.

FIGURE 226.—*Tyche emarginata* White. Left outer maxilliped (after Garth, 1946).

Chelipeds of male more than twice length of postorbital part of carapace; palms somewhat dilated and compressed; fingers gaping at base, dentate throughout length. Walking legs ornamented with stout hooked hairs; dactyls spinulous on middle third, spinules increasing in size distally.

Abdomen of both sexes with seven free segments.

Measurements.—Carapace: female, length, 35 mm.; width, 21 mm.

Color.—Generally yellowish gray; carapace greenish above, with two triangular white spots; blackish above base of legs (various authors).

Habitat.—The species has been reported from rocky or coarse shell bottoms (Rathbun, 1925); a few feet to 20 fathoms.

Type locality.—West Indies.

Known range.—Off Beaufort Inlet, N.C.; through Bahamas to west coast of Florida; Cape São Roque, Rio Grande do Norte, Brazil.

Remarks.—Garth (1946) gave a detailed comparison of this species with its Pacific counterpart, *T. lamellifrons.*

Subfamily **Acanthonychinae**

Eyes without true orbits; eyestalks very short or sometimes obsolescent, either concealed beneath an anteriorly produced supraocular spine, or sunk in sides of a huge beaklike rostrum; a postocular spine or process sometimes present, but not excavated for reception of retracted eye. Basal antennal article elongate but truncate-triangular. External maxillipeds with merus as broad as ischium. Dactyls of walking legs prehensile or subchelate; last three pairs of legs often disproportionately short compared with [first] pair (Alcock, 1895). Postocular spine not cupped (except in *Sphenocarcinus*); rostrum either simple or two-spined; palp on third maxilliped arising from anterointernal angle of merus (Rathbun, 1925). First pleopod medium stout, apex most varying (hammer-shaped; divided into three or four lobes; etc.); second pleopod short (Stephensen, 1945).

KEY TO GENERA OF ACANTHONYCHINAE IN THE CAROLINAS

a. Rostrum double; seven free abdominal segments in both sexes ..... *Sphenocarcinus* (p. 248).

aa. Rostrum single or secondarily bifurcate; six free abdominal segments in male, five in female ..... *Epialtus* (p. 249).

Genus ***Sphenocarcinus*** Milne Edwards, 1878

Garth, 1958, p. 217.

Sphenocarcinus corrosus Milne Edwards

Figures 227, 233C

Sphenocarcinus corrosus Milne Edwards, 1875, pl. 17, figs. 5–5c.—Hay and Shore, 1918, p. 460, pl. 39, fig. 1.—Rathbun, 1925, p. 187, text-fig. 73, pl. 62; pl. 223, figs. 3–5 (rev.).

Recognition characters.—Carapace subpentagonal, broad behind, anterolateral margin concave, posterolateral margin convex. Dorsal surface deeply channeled, leaving symmetrical, coarsely punctuate, or eroded elevations in regular pattern as follows: a longitudinally placed, trefoil-shaped gastric, a transversely placed cardiac with two deep posterior indentations, a transversely elongate intestinal, paired laterals extending from near lateral angles to near eyes, and paired small postocular and larger supraocular elevations; margins of all elevations sharply defined with surface finely eroded. Rostrum usually longer than carapace, formed of two pointed horns contiguous to near tips, slightly divergent in old individuals. Eye deeply sunk between two low smooth excrescences. Basal antennal article truncate, antennal flagellum hidden beneath rostrum. Epistome long, narrow.

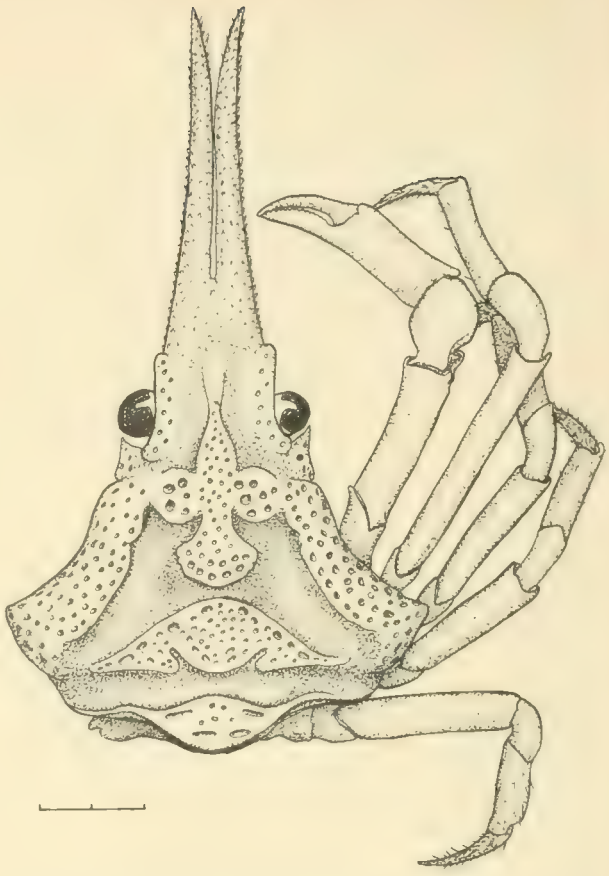

FIGURE 227.—*Sphenocarcinus corrosus* Milne Edwards. Male in dorsal view, legs of left side not shown, 2 mm. indicated.

Chelipeds weak; first pair of walking legs longer than others and exceeding length of chelipeds by more than length of dactyl.

Abdomen in both sexes with seven distinct segments.

Measurements.—Carapace: male, length, 13 mm., width, 7 mm.; ovigerous female, length, 23 mm., width, 11 mm.

Variations.—Divergence of the rostral horns varies individually. In some specimens the horns are contiguous nearly to the tip, in others the horns may be divergent for half their length, and in still others there is no evidence at all of bifurcation.

Color.—Orange-red.

Habitat.—Ninety to 148 fathoms.

Type locality.—Off Barbados, 100 fathoms.

Known range.—Off Cape Lookout, N.C., to Barbados.

Remarks.—Ovigerous females have been reported from North Carolina in April (Rathbun, 1925).

Genus ***Epialtus*** H. Milne Edwards, 1834

Garth, 1958, p. 227.

Epialtus dilatatus Milne Edwards

Figures 228, 233D

Epialtus dilatatus Milne Edwards, 1878, p. 140, pl. 27, figs. 4–4b.—Rathbun, 1925, p. 153, text-fig. 53j, pl. 45, fig. 2 (rev.).

Recognition characters.—Small species. Carapace broad, subpentagonal, almost smooth, with hepatic and branchial projections more or less laminate. Rostrum broad, somewhat triangular, short, bilobed at tip, slightly depressed on median line dorsally with depression continued ventrally and limited by two crests uniting posteriorly in an acute angle. Eyes small; preorbital angles scarcely marked; postorbital teeth minute. Basal article of antenna triangular, movable part concealed beneath rostrum.

Chelipeds moderate in size; carpus with four longitudinal crests; hand slightly enlarged distally, upper margin blunt, defined by depression on either side; fingers short and stout. Walking legs with slight tuft of hair on lower margin of propodi.

Abdomen of male with six, female with five, free segments.

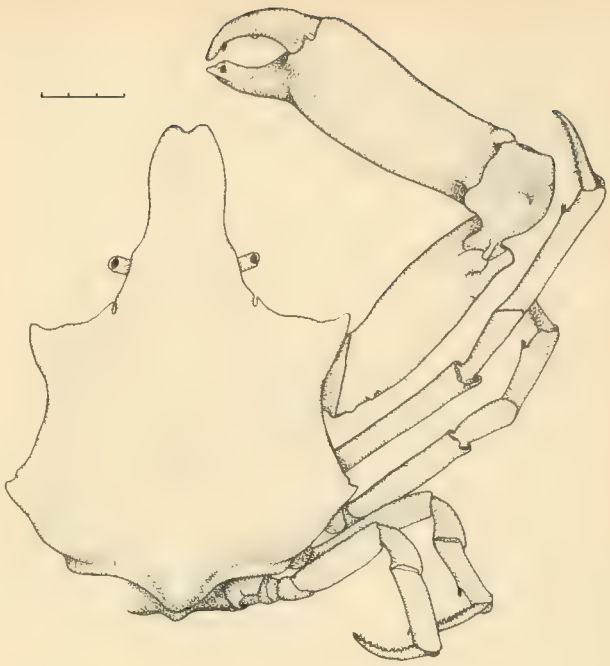

FIGURE 228.—*Epialtus dilatatus* Milne Edwards. Male in dorsal view, legs of left side not shown, 3 mm. indicated.

Measurements.—Carapace: male, length, 17 mm., width, 13 mm.; female, length, 10 mm., width, 8 mm.

Variations.—Members of the genus *Epialtus* are variable in a number of respects. The hepatic expansion may vary in shape and the rostrum may vary from triangular to suboblong in shape.

Rathbun (1925) recognized from southwestern Florida an elongate form which has a longer rostrum and slightly different lateral expansions than the typical form.

Habitat.—The species has been reported from shell reefs and coarse coral sand, and the elongate form has been found on sandy-grassy bottoms as well. Two and one-half to 12 fathoms.

Type locality.—St. Thomas.

Known range.—Off Beaufort Inlet and New River, N.C.; southwest Florida; Yucatan; Bahamas to St. Thomas.

Remarks.—Rathbun (1925) reported ovigerous females from Florida in April. They are known from North Carolina in June, and in Florida through the summer. Other records are Brazil in September, and Puerto Rico in November (U.S. National Museum records).

Subfamily **Pisinae**

Eyes with commencing orbits, eye retractile into sometimes large, blunt, usually isolated, cupped postocular tooth or lobe, but never to such extent as to conceal completely cornea from dorsal view; usually a prominent supraocular eave with anterior angle sometimes produced forward as a spine; eyestalks short. Basal antennal article broad, at least at base, anterior angle generally produced to form a tooth or spine. Merus of external maxilliped broader than ischium owing to expansion of anteroexternal angle, and carrying palp at anterointernal angle. Rostrum [except in *Neodoclea* among New World forms] two-spined; legs often very long (Alcock, 1895). First pleopod medium stout to slender, usually apically somewhat tapering, but apex extremely varying (blunt, acute, filiform, straight, geniculate, etc.); second pleopod short (Stephensen, 1945).

KEY TO GENERA OF PISINAE IN THE CAROLINAS

Modified after Garth (1958)

a. Intercalated orbital spine present.....*Nibilia* (p. 251).
aa. Intercalated orbital spine absent.
  b. Supraocular eave and postocular process not closely approximated.....*Pelia* (p. 250).
  bb. Supraocular eave and postocular process closely approximated.....*Libinia* (p. 251).

Genus ***Pelia*** Bell, 1835

Garth, 1958, p. 268.

Pelia mutica (Gibbes)

Figures 229, 233E

Pisa mutica Gibbes, 1850, p. 171.
Pelia mutica: Hay and Shore, 1918, p. 455, pl. 38, fig. 7.—Rathbun, 1925, p. 278, text-fig. 94, pl. 98, figs. 2–3 (rev.).

Recognition characters.—Small species. Carapace pyriform, greatest width approximately two-thirds greatest length, swollen, devoid of tubercles, covered with sparse pubescence, gastric and cardiac regions elevated. Rostrum well developed, two-fifths as long as remainder of carapace, formed of two more or less distally divergent horns with outer margins often parallel, a furrow on basal portion. Eyes retractile. Basal antennal article long, slender, forming incomplete floor to orbit and jutting out beyond orbital margin, usually with small tooth or spine at anteroexternal angle; antennal flagellum greatly developed.

FIGURE 229.—*Pelia mutica* (Gibbes). Animal in dorsal view, legs of right side not shown, 3 mm. indicated.

Chelipeds of mature male as long as first walking legs but stouter and almost bare, weaker in females and young males; upper and inner margin of merus dentate; carpus with a longitudinal denticulate ridge; upper and lower margins of hand slightly arcuate; basal half of fingers widely agape, with denticulate margins on occludent portions and broad basal tooth of dactyl; fingers weaker and not agape in females and young males. Walking legs with marginal rows of stiff setae, meri much compressed, dactyls strongly curved.

Abdomen of both sexes with seven free segments.

Measurements.—Carapace: male, length, 13 mm., width, 9 mm.; ovigerous females, length, 5–10 mm. (Wass, 1955).

Color.—Bright red in patches on carapace and in bands on legs, spots of light red on chelipeds (Rathbun, 1925).

Habitat.—This species has been found on gravelly and shelly bottoms of bays and sounds, among hydroids, ascidians, and sponges on wharf piles, and also on shelly reefs off Beaufort Inlet,

N.C. (Pearse and Williams, 1951). Individuals are often so covered with sponge that they are difficult to recognize. Gray (1961) reported the species from *Chaetopterus* tubes. Low water to 28 fathoms.

Type locality.—Charleston Harbor, off White Point Battery, S.C.

Known range.—Buzzards Bay and Vineyard Sound, Mass., to west coast of Florida; Cuba, Puerto Rico, and St. Thomas, West Indies.

Remarks.—Ovigerous females are known from February to July in Florida, through the summer in the Carolinas, and in Massachusetts in July (Rathbun, 1925; U.S. National Museum records).

Genus ***Nibilia*** Milne Edwards, 1878

Rathbun, 1925, p. 289.

Nibilia antilocapra (Stimpson)

Figures 230, 233F

Pisa antilocapra Stimpson, 1871a, p. 110.
Nibilia antilocapra: Rathbun, 1925, p. 290, text-fig. 97, pls. 102, 103, and 239 (rev.).

Recognition characters.—Carapace pyriform, conspicuously spinose, much swollen, longer than wide; gastric and cardiac regions with about 18 spines of moderate size and smaller ones interspersed, largest spines surmounting summit of regions and somewhat surrounded by circle of smaller spines; other regions also well spined.

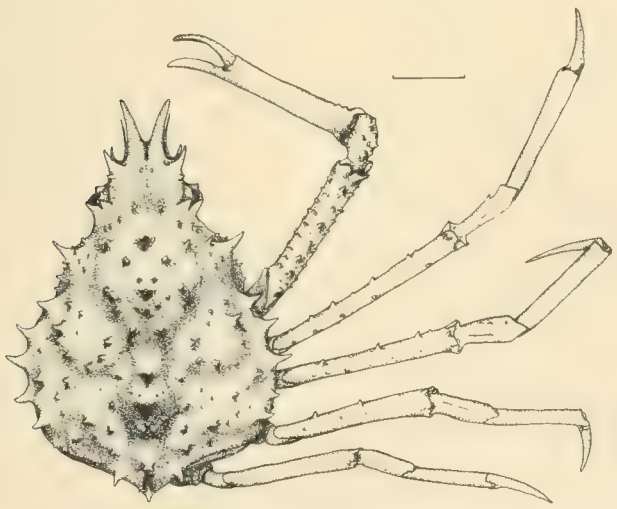

FIGURE 230.—*Nibilia antilocapra* (Stimpson). Male in dorsal view, legs of left side not shown, 10 mm. indicated.

Rostrum horizontal, undivided at base but moderately bifurcate for greater part of length, horns varying from three-fifths to four-fifths total length of rostrum. Preorbital spine ascending, slightly curved, not so advanced as base of horns; behind this a small spine on supraocular eave and a triangular (intercalated) spine or tooth on supraocular border; postocular cup terminating in a spine. Basal antennal article with a short spine just outside posterior end, behind this a tubercle in line with prominent spine at angle of buccal cavity. Maxilliped and sternum smooth.

Chelipeds of adult male longer and stouter than walking legs; merus and carpus rough with spines above and below; chelae almost cylindrical; hand nearly as long as merus, nearly smooth, a few spines near articulation with carpus; fingers agape for half of length in old males, with a well-developed tooth on dactyl in gaping part. Walking legs long, slender; merus and carpus with a few spines longitudinally arranged; dactyls long, stout, unarmed.

Measurements.—Carapace: large male, length, 120 mm., width, 82 mm.; female, approximate length, 60 mm., width, 43 mm.

Variations.—The young and half-grown are covered with short hair, but the old are nearly bare except for hairy dactyls on the walking legs.

Habitat.—The species has been reported from gray and coarse sand, broken-shell, and coral bottoms (Rathbun, 1925); 39 to 140 fathoms.

Type localities.—Florida, off Carysfort Reef, 52 and 60 fathoms; and off Alligator Reef, 118 fathoms.

Known range.—Off Cape Hatteras, N.C., to Gulf of Mexico just east of Mississippi River Delta and Gulf of Campeche; Windward Islands, West Indies.

Remarks.—Ovigerous females have been reported from St. Vincent in February and from Barbados in March (Rathbun, 1925).

Genus ***Libinia*** Leach, 1815

Garth, 1958, p. 322.

KEY TO SPECIES IN THE CAROLINAS

a. Median line of carapace with about nine spines *emarginata* (p. 252).
aa. Median line of carapace with about six spines *dubia* (p. 252).

Libinia emarginata Leach. Spider crab

Figures 231, 233H

Libinia emarginata Leach, 1815, p. 130, pl. 108.—Hay and Shore, 1918, p. 456, pl. 38, fig. 6.—Rathbun, 1925, p. 311, text-figs. 103–104; pls. 110–113 (rev.).

Recognition characters.—Carapace orbicular, about one-sixth longer than wide, spinose and tuberculate, with dense covering of short hairs. Larger spines arranged as follows: median row of about nine extending from near base of rostrum to posterior border consisting of four gastric, one genital, two cardiac, and two intestinal; lateral marginal spines five on each side; two subhepatic spines; two or four spines above posterior margin, aside from median spine, and about four dorsal branchial spines; spiniform tubercles scattered about among larger spines. Gastric region marked off by a deep groove. Rostrum slightly depressed, emarginate or bifid at tip; a median groove between eyes. Orbits with prominent preorbital spine, two spines beneath on basal article of antenna; one fissure above and one beneath.

Chelipeds equal, larger in male; hands granulate; fingers smooth, evenly denticulate, and about half as long as hand. Walking legs long, hairy, unarmed, often unequal and asymmetrical (result, perhaps, of injury and subsequent regeneration).

Measurements.—Carapace: male, length, 103 mm., width including spine, 94 mm.; female, length, 62 mm., width, 58 mm.

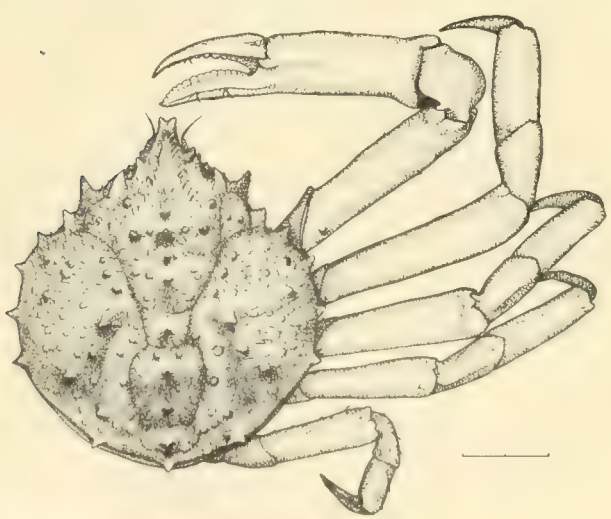

FIGURE 231. *Libinia emarginata* Leach. Male in dorsal view, legs of left side not shown, 20 mm. indicated.

Variations.—The number of median spines in the gastric region is subject to some variation in size and number.

Color.—A brownish or dirty yellow.

Habitat.—Found on almost any kind of bottom; shore to 27, occasionally 68, fathoms.

Type locality.—Unknown.

Known range.—Windsor, Nova Scotia, to western Gulf of Mexico.

Remarks.—Hildebrand (1954) reported this species as the most common large spider crab in the western Gulf of Mexico. It was most common in July, at which time ovigerous females were observed. Another ovigerous female was taken in February. (Elsewhere ovigerous females are known from New Jersey in August (U.S. National Museum records).) Hildebrand also observed juveniles riding in the bell of scyphozoan *Stomolophus meleagris*, a habit noted by others for the young of *L. dubia*.

The young of *L. emarginata* and *L. dubia* are difficult to distinguish. Wass (1955) pointed out useful distinguishing marks. "The rostrum of *L. dubia* is much longer, forming a V; the carapace is not so wide, and there is but one spine on the intestinal region . . . whereas *L. emarginata* has two."

Gray (1957) compared gill area in this sluggish species with that of other common littoral crabs in the Carolinas and found that it had the smallest gill area per gram body weight of any studied.

Libinia dubia H. Milne Edwards. Spider crab

Figures 232, 233G

Libinia dubia H. Milne Edwards, 1834, p. 300, pl. 14*bis*, fig. 2.—Hay and Shore, 1918, p. 456, pl. 38, fig. 5.—Rathbun, 1925, p. 313, text-figs. 105–106; pls. 114–115; pl. 122, fig. 1 (rev.).

Recognition characters.—Similar in general characters to *L. emarginata* but with more pyriform carapace and fewer spines; median row with but six spines, two gastric, one genital, two cardiac, and one intestinal; preorbital, subhepatic, and lateral spines stronger than in *L. emarginata*, but spiniform tubercles few or wanting altogether. Rostrum slightly longer and more definitely bifid than in *L. emarginata*. Anterolateral angle of buccal frame armed with a spine.

Measurements.—Carapace: male, length, 102 mm.; width including spines, 82 mm. Most individuals smaller.

Variations.—Dorsal spines and tubercles variable in length.

Habitat.—Found on almost all types of bottom in the ocean and the saltier sounds. Occasionally, large individuals are found on Bird Shoal near Beaufort, N.C., in pools left by falling tide; frequently specimens are brought up in otter trawls. Immature individuals are often completely overgrown with sponges, hydroids, or ascidians, but the larger ones are usually almost clean. Near shore to 25 fathoms.

Type locality.—Côtes des Etats-Unis.

Known range.—Cape Cod, Mass., to southern Texas; Bahamas and Cuba.

Remarks.—This species has a geologic record extending from the upper Miocene of Virginia (Rathbun, 1935) through the Pleistocene of New

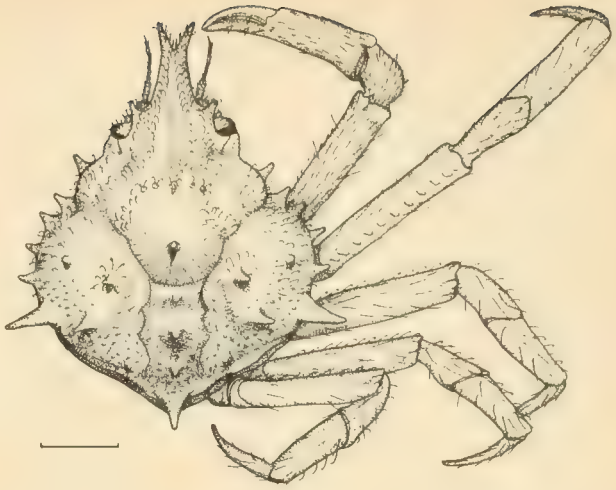

FIGURE 232.—*Libinia dubia* H. Milne Edwards. Male in dorsal view, legs of left side not shown, 10 mm. indicated.

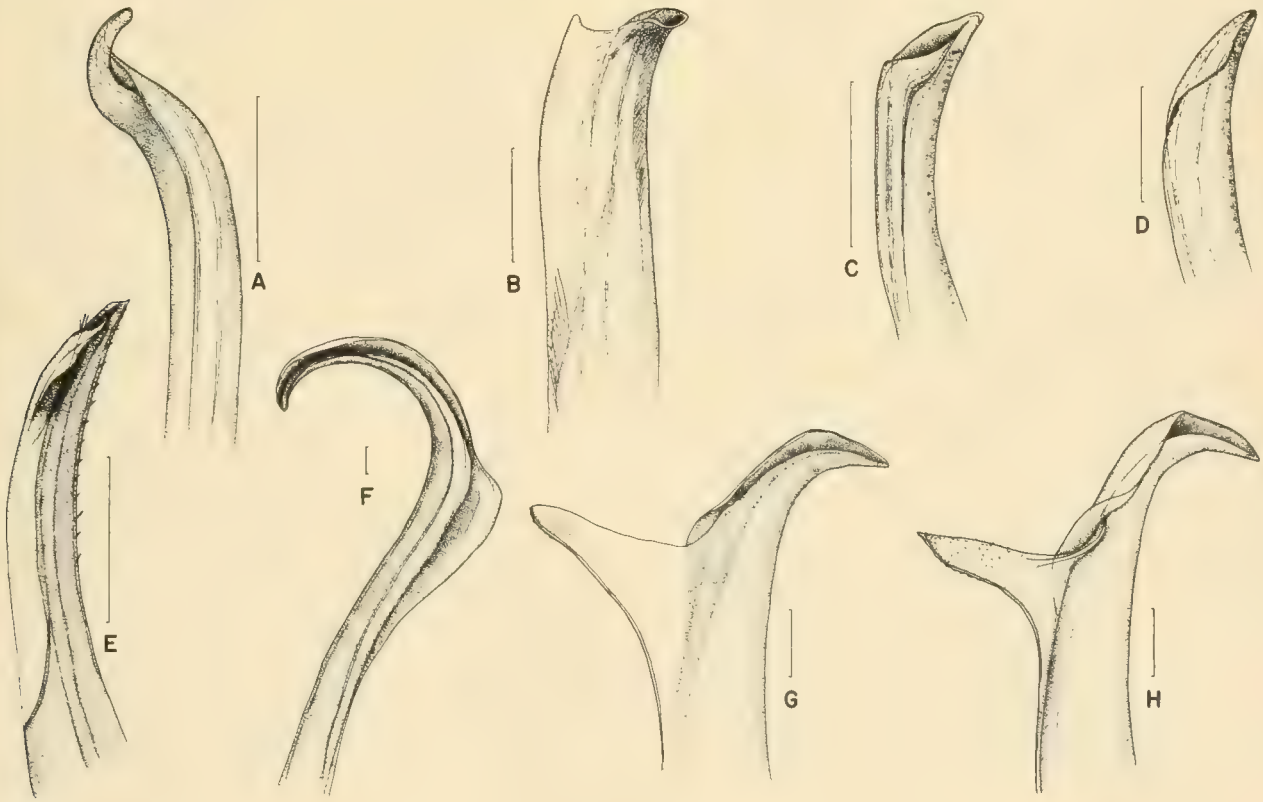

FIGURE 233.—Subfamilies Ophthalmiinae, Acanthonychinae, and Pisinae, tips of right first pleopods of males; A, *Pitho lherminieri* (Schramm), abdominal view; B, *Tyche emarginata* White, lateral view; C, *Sphenocarcinus corrosus* Milne Edwards, sternal view; D, *Epialtus dilatatus* Milne Edwards, sternal view; E, *Pelia mutica* (Gibbes), sternal view; F, *Nibilia antilocapra* (Stimpson), abdominal view; G, *Libinia dubia* H. Milne Edwards, lateral view; H, *Libinia emarginata* Leach, lateral view; 0.33 mm. indicated.

Jersey (Rathbun, 1935) and Maryland (Easton, 1940).

Ovigerous females are known to occur in spring in North Carolina.

Pearse (1929), studying the survival rates of various estuarine crabs in dilutions of sea water and in air, found *L. dubia* least able to survive desiccation and dilutions of sea water. Ayers (1938), in a study of the relationship of habitat to oxygen consumption among certain estuarine crabs, found that *L. dubia* lives much of the year in relatively deep [estuarine] water where there is low oxygen content, sometimes very little. The species is correspondingly sluggish and slow. Gray (1957) showed that gill area per gram of weight in this species is small.

A peculiar association of this species with the jellyfish *Stomolophus meleagris* has been reported. The crabs have been found in the subumbrellar space and on occasion small specimens have been taken from the genital pits. Corrington (1927) found medusae with crabs between Sullivans Island and Isle of Palms, S.C., in May, and Gutsell (1928) found the association in the vicinity of Cape Lookout, N.C., in summer and fall. The crabs were found in adult jellyfish and varied in length from 3 to 37 mm.

Pearse (1952b) reported *Octolasmis lowei* (=*mulleri*) on the gills and mouth parts, and *Chelonibia patula* on the carapace of *L. dubia* in Texas.

Subfamily **Mithracinae**

Carapace broadened anteriorly by outstanding, often tubular, orbits; orbits formed (1) by an arched supraocular hood, or semitubular horn, (2) by a hollowed postocular process, and (3) by a remarkable broadening, or by a prolongation, of anterior part of basal antennal article, affording complete concealment to retracted eye. Rostrum often more or less deflexed (Alcock, 1895). First pleopod like that in Pisinae; second pleopod short (Stephensen, 1945).

KEY TO GENERA OF MITHRACINAE IN THE CAROLINAS

Modified after Garth (1958)

a. Intercalated orbital spine present (between supraorbital and postorbital spine); orbits projecting somewhat beyond general outline of carapace, but not tubular.

b. Rostrum small; carapace ovate, usually broader than long ..... *Mithrax* (p. 254).

bb. Rostrum large, usually with two strong horns; carapace broadly pyriform; basal antennal article armed with a prominent spine at anteroexternal angle ..... *Microphrys* (p. 259).

aa. Intercalated orbital spine absent; orbits tubular.

b. Lateral margin of carapace armed with series of strong spines; basal antennal article very broad ..... *Stenocionops* (p. 260).

bb. Lateral margin of carapace not armed with series of strong spines, but with a spine, usually strong, at lateral angle of carapace ..... *Macrocoeloma* (p. 263).

Genus ***Mithrax*** Desmarest, 1823

Garth, 1958, p. 352.

KEY TO SPECIES IN THE CAROLINAS

(Modified from Garth, 1958, and Rathbun, 1925)

a. Carapace roughened to greater or lesser extent by tubercles or spinules, branchial grooves wanting; intermediate orbital teeth conspicuous, pointed, or subtruncate ..... (Subgenus *Mithrax*).

b. Hand armed above with spines or spinules.

c. Two spines only on basal (fused) article of antenna ..... *spinosissimus* (p. 254).

cc. Three spines on basal (fused) article of antenna; carapace paved with flattened granules, concealed by short hair ..... *verrucosus* (young) (p. 255).

bb. Hand not armed above with spines or spinules.

c. Carapace paved with close-set, tessellated granules ..... *verrucosus* (p. 255).

cc. Carapace not paved with close-set, tessellated granules.

d. Gastric region without definite transverse row of five tubercles ..... *hispidus* (p. 256).

dd. A transverse row of five tubercles across gastric region ..... *pleuracanthus* (p. 257).

aa. Carapace smooth and bearing oblique branchial grooves, either strongly or weakly indicated; intermediate orbital teeth inconspicuous, tuberculiform (Subgenus *Mithraculus*).

Carapace broader than long; anterolateral margins cut into spines, or angular lobes, or spines and lobes; four anterolateral protuberances behind orbit ..... *forceps* (p. 258).

Mithrax (Mithrax) spinosissimus (Lamarck)

Figures 234, 245A

Maia spinosissima Lamarck, 1818, p. 241.
Mithrax spinosissimus: Rathbun, 1925, p. 383, pl. 135 (rev.).

Recognition characters.—Large. Carapace nearly naked, subcircular, approximately as broad as long; surface rough with short spines, those in center blunt, elsewhere sharp; cervical suture deep; hepatic and cardiac regions distinctly delimited. Rostral horns narrow, obliquely truncate and granulate at extremity, separated by a U-

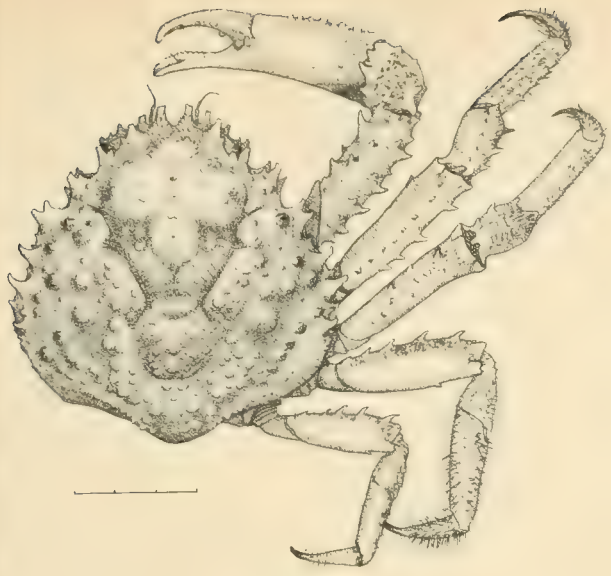

FIGURE 234.—*Mithrax* (*Mithrax*) *spinosissimus* (Lamarck). Male in dorsal view, legs of left side not shown, 30 mm. indicated.

shaped notch of equal length and breadth; two stout spines at base of horns and two more behind these but farther apart; preorbital spine stouter, truncate, and less advanced than rostrum. Orbital border with three small teeth exclusive of postorbital spine; suborbital margin with one acute spine outside antennal segment and lateral to this a larger truncate spine. Antennal segment with an outer small acute spine and an inner spine more advanced than rostrum bearing a small secondary lateral spine near end. Lateral margin with six spines, first two double, last and smallest one on posterolateral margin. Other spines present on suborbital, subhepatic, subbranchial, pterygostomian regions, and at angle of buccal cavity.

Chelipeds of adult male massive, longer than walking legs; merus armed with eight or nine stout spines on outer margin, others irregularly placed; carpus armed with unequal spines, about five on inner margin; hand deep, compressed, armed above with a more or less double row of spines and on inner surface with two to four spines proximally; fingers curved leaving wide gape, strong tooth near middle of dactyl, tips spooned with edges crenate preceded by a few low tubercles. Adult female with chelipeds no longer and not much stouter than first pair of walking legs; hand tapering somewhat distally; fingers narrowly gaping with numerous denticles on cutting edges. Walking legs of both sexes spinose and coarsely hairy; propodi elongate and compressed.

Abdomen of male with seven free segments, female with six.

Measurements.—This is the largest species of *Mithrax*. Carapace: male, length, 170 mm., width, 184 mm.; female, length, 77 mm., width, 80 mm.

Variations.—In old males, spines on the chelipeds tend to become blunt and tuberculiform. In medium-sized individuals, the carapace is relatively longer than in the old, spines are sharper, rostral horns curve inward at the sharp tips, the carapace is covered with short hair, chelipeds of both sexes are small, and the gape extends only half the length of the fingers. In young individuals, the spines are even more accentuated, rostral horns are one-fifth as long as the carapace, there are two spines on the suborbital margin outside the antennal segment, chelipeds are no longer or stouter than the first walking legs, and gape of the fingers is less than in older individuals.

Color.—Bright carmine; vinous red with yellowish tints; or thorax dark red; walking legs brick red and chelipeds rose red with yellow fingers (various authors including Rathbun, 1925).

Habitat.—The species is often found among rocks. The carapace is often covered with encrusting organisms; shallow water to 98 fathoms.

Type locality.—Ile-de-France. Locality erroneous.

Known range.—Either North Carolina or South Carolina (?) through Florida Keys and West Indies to Guadeloupe.

Remarks.—Ovigerous females have been reported in May and June from Cuba (Rathbun, 1925).

Mithrax (Mithrax) verrucosus H. Milne Edwards

Figures 235, 245B

Mithrax verrucosus H. Milne Edwards, 1832, cl. 7, pl. 4 (col.) [+ unpaginated description].—Rathbun, 1925, p. 400, pl. 144 (rev.).

Recognition characters.—Mature males, large- to medium-sized. Carapace covered with flattened, closely crowded granules, nearly naked, granules covered with small pits, cervical suture deep; branchial region with a few dorsal spines on outer part, front and orbit with truncate spines. Rostral

FIGURE 235.—*Mithrax (Mithrax) verrucosus* H. Milne Edwards. Male in dorsal view, legs of left side not shown, 20 mm. indicated.

horns short, separated by a deep notch. Preorbital spine directed somewhat outward, four other spines on orbital margin aside from three occurring on broad basal antennal article. Anterolateral margin with eight spines, first six in pairs, anterior spines of each pair smaller, spines in first two pairs more or less united at base; a single posterolateral spine, and below lateral margin a row of about nine spines.

Chelipeds stout; outer margin of merus with six sharp spines, approximately six spines on upper surface; inner margin of whole cheliped armed with blunt spines or lobes, one on ischium, four on merus, two or three on carpus; carpus with dorsal surface smooth or slightly tuberculate proximally; palm unarmed, elongate, somewhat swollen, fingers gaping with a large tooth near middle of dactyl, edges of spoon-shaped tips slightly crenulate, two bunches of hair inside spoon. Walking legs covered with coarse hair, meri and carpi spiny.

Measurements.—Carapace: male, length, 51 mm.; width, 65 mm.

Variations.—Females, young, and most immature males differ from mature males in that the carapace is covered densely with hair. Rostral horns of females and immature males are shorter and further apart, but horns of the young are sharper. Spines on the inner margin of the chelipeds are sharper, the carpus is more or less spiny dorsally, and the palm is spinulous and hairy above proximally. The degree of spination on the chelipeds also varies individually.

Color.—Dark red; color largely concealed by hairiness, carapace dark dull red, pincers olive above and lighter olive below, tips claret, teeth white, underparts maroon flecked with white and yellow (various authors and Rathbun, 1925).

Habitat.—This species lives near shore among rocks, where it hides in holes. It is nocturnal, and has been caught with the aid of a light while feeding. Shallow water near shore.

Type locality.—Robert Bay, Martinique.

Known range.—Charleston, S.C., through West Indies to Fernando Noronha Island (225 miles northeast Cape São Roque), Brazil.

Remarks.—Pearse (1932a) determined freezing point of blood in this species at Tortugas (range −1.99° to −2.24° C.).

Mithrax (Mithrax) hispidus (Herbst). Coral crab

Figures 236, 245C

Cancer hispidus Herbst, 1790, p. 245 (247 by error), pl. 18, fig. 100.

Mithrax hispidus: Rathbun, 1925, p. 406, text-fig. 124, pls. 145–146; pl. 147, fig. 3 (rev.).

Recognition characters.—Carapace swollen, considerably wider than long, smooth except for some low, rounded prominences chiefly toward outer margin of branchial region, gastric tubercles

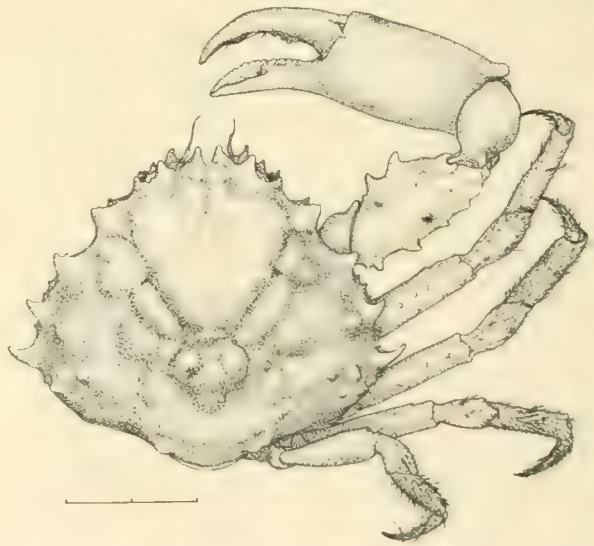

FIGURE 236.—*Mithrax (Mithrax) hispidus* (Herbst). Male in dorsal view, legs of left side not shown, 20 mm. indicated.

faint; front wide. Rostral horns short, obtuse, separated by a U-shaped notch. Preorbital angle blunt, slightly produced. Basal article of antenna with two teeth, inner one nearly as advanced as rostrum, outer smaller one on orbital border. Orbit with four tubercles on margin, two superior much smaller than external or inferior ones. Anterolateral margin with four spiniform teeth, first one obtuse, often bifid at tip; second longer, sharp, double, and curving forward; third and fourth slender. Posterolateral border with a smaller tooth situated higher on carapace in line with two obliquely located tubercles, or a low spine and a tubercle. Subhepatic region with two tubercles; a few other tubercles on subbranchial and pterygostomian regions.

Chelipeds large, unequal in males, equal in females; merus with four or five spines and a few tubercles on upper surface and two spines on inner margin; carpus smooth; hand smooth; fingers spooned at tips, gaping, with a broad low crenulated tooth near base of dactyl.

Measurements.—Carapace: large male, length, 102 mm.; width, 146 mm.

Variations.—Young individuals have tubercles on the carapace more protuberant than in the old.

Color.—Nearly uniform deep brownish-red or terra cotta color above, brighter on chelipeds and darker on legs (due to brown hairs); legs often with brighter red bands at joints; underparts of body mostly white or bluish white; legs red, speckled with pale yellow (Verrill, 1908).

Habitat.—Commonly lives on rough bottom; shallow water to 30 fathoms.

Type locality.—Unknown.

Known range.—Recorded in literature from as far north as Delaware Bay (Say, 1818), off Charleston Harbor, S.C., and Georgia (Gibbes, 1850). Bahamas and Florida Keys through West Indies to São Paulo, Brazil; Bermuda.

Mithrax (Mithrax) pleuracanthus Stimpson

Figures 237, 245D

Mithrax pleuracanthus Stimpson, 1871a, p. 116.—Milne Edwards, 1875, p. 95, pl. 20, figs. 3–3f.—Rathbun, 1901, p. 68.—Hay and Shore, 1918, p. 458, pl. 38, fig. 3.—Rathbun, 1925, p. 411, pl. 150 (rev.).

Mithrax depressus Milne Edwards, 1875 (in part), p. 96, pl. 20, figs. 4–4c.—Rathbun, 1901, p. 68.—Verrill, 1908, p. 407, pl. 23, fig. 1.—Hay and Shore, 1918, p. 458, pl. 38, fig. 2.

Mithrax hispidus Rathbun, 1892 (in part), p. 265.

Recognition characters.—Carapace not much wider than long, conspicuously tuberculate; front

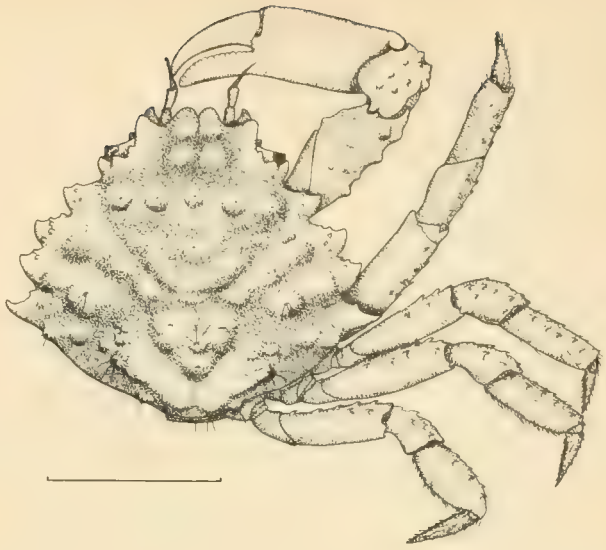

FIGURE 237.—*Mithrax (Mithrax) pleuracanthus* Stimpson. Animal in dorsal view, legs of left side not shown, 10 mm. indicated.

wide. Rostral horns shorter and wider than in *M. hispidus*, notch between horns narrower and nearly triangular, always triangular in young individuals. Preorbital angle blunt, slightly produced; orbit with two superior tubercles; a small postorbital angle and a suborbital tubercle. Basal article of antenna with two teeth, inner one nearly as advanced as rostrum, outer smaller one on orbital border. Spines of anterolateral border well developed, anterior one or two inclined to be double, posterior two more acute and pointed forward, small tubercles about base of spines. Gastric region with transverse row of five tubercles, in front of these, two pairs of tubercles, anterior pair at base of rostral horns. Mesogastric region with two tubercles on each side in a transverse line. Cardiac region with three poorly defined tubercles. Branchial area with four rather strong tubercles and several smaller ones arranged more or less in three oblique rows radiating from cardiac region to anterolateral border.

Chelipeds large; merus with scattered low spines on upper margin, with a simple spine, spine and tubercle, or rounded eminence on inner margin, and five small spines on posterior border; carpus smooth or with a few low tubercles on upper surface; hands smooth; fingers slightly gaping, dentate for nearly entire length, spoon-shaped at tips. Walking legs dentate and hairy.

Measurements.—Carapace: large male, length, 36 mm., width, 43 mm.; ovigerous female, length, 16 mm., width, 19 mm.

Variations.—In young individuals the rostral horns are wider behind and flatter than in adults; the notch between the rostral horns in extremely large individuals may be U-shaped; the large tubercle above the posterolateral margin may be spiniform but is located higher on the carapace than the similarly formed tubercle in *M. hispidus.*

Color.—Carapace yellowish white, with blotches of bright red; two largest red spots over branchial areas, a median spot on cardiac area, a pair situated farther back, a small pair behind orbits, and another beneath orbits; legs yellowish white, blotched or barred with red; chelae light red with pale tips (Verrill, 1908, for *M. depressus*).

Habitat.—This species, which is often encrusted with bryozoans and other organisms, is found predominantly on coarse or rocky substrates but occasionally on muddy or sandy bottom. In North Carolina it is a common species on the offshore banks and is associated with *Mithrax forceps.* Pearse (1934) found the species in canals of the sponge *Stematumenia strobilinia* (Lamarck) at Tortugas, Fla. Shallow water to 28 fathoms.

Type localities.—Key West, 2–5 fathoms, Tortugas, 5–6 fathoms [Fla.]; St. Thomas.

Known range.—Beaufort, N.C., to Pensacola, Fla.; Yucatan Channel off Cape Catoche, Mexico, and Gulf of Campeche; West Indies to Venezuela; Bermuda.

Remarks.—Ovigerous females are known in Florida from December to February, and in August. They are known from North Carolina in April, St. Thomas in July, and Venezuela in September (Rathbun, 1925; U.S. National Museum records).

Mithrax (Mithraculus) forceps (Milne Edwards)

Figures 238, 245E

Mithraculus forceps Milne Edwards, 1875, p. 109, pl. 23, fig. 1.
Mithrax forceps: Hay and Shore, 1918, p. 457, pl. 38, fig. 1 Rathbun, 1925, p. 431, pl. 156 (rev.).

Recognition characters.—Carapace about one-fifth wider than long, deeply sculptured in young individuals but smoother with age. Anterolateral margin with four tubercles or teeth exclusive of postorbital angle, separated by broad rounded sinuses, first tooth usually shortest, remainder usually acute and turned forward at tip. Three

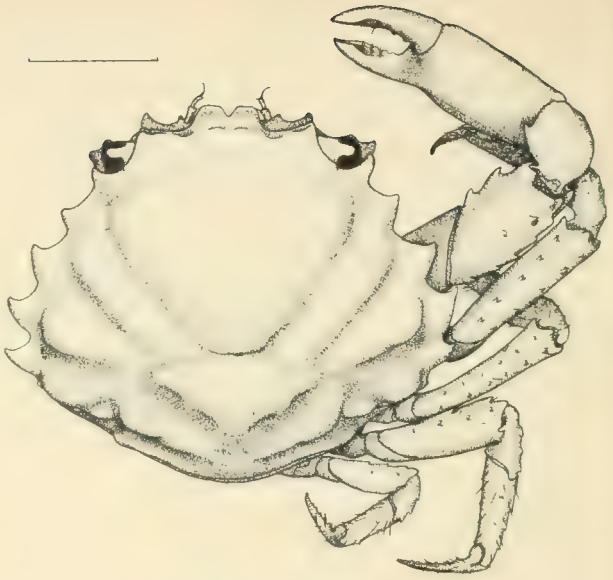

FIGURE 238.—*Mithrax (Mithraculus) forceps* (Milne Edwards). Male in dorsal view, legs of left side not shown, 5 mm. indicated.

grooves running diagonally backward over branchial area from near first, second, and fourth sinuses of anterolateral margin, between these grooves two well-defined, unbroken ridges and a broken ridge behind third groove. Cardiac and gastric regions crossed by less sharply defined ridges somewhat broken up into low rounded tubercles. Notch between rounded rostral horns broadly V-shaped, two pairs of tubercles on frontal region behind lobes of rostrum. Preorbital angle prominent, not exceeding rostrum. Orbital margin with a dorsal and ventral tubercle near postorbital angle. Outer spine of fused antennal article nearly equaling rostrum.

Chelipeds strong. Merus with two strong spines or tubercles in front, five much smaller ones on posterior margin, and usually two on upper surface near posterior margin. Carpus smooth or with a small spine or tubercle on inner margin near inner distal angle. Hand smooth, polished, somewhat tumid. Fingers widely gaping in male, with expanded hollowed-out tips; dactyl with single large tooth one-third distance from proximal end, or with a few minute teeth; immovable finger with from one to three small teeth or tubercles in middle. Walking legs spiny or denticulate with many fine hairs.

Measurements.—Carapace: male, length, 21 mm.; width, 25 mm.

Color.—Red, approaching vermilion, with occasional trace of purple. Terra cotta, or uniform yellowish brown, varying to greenish brown; often with a wide, pale yellow, median dorsal stripe, and legs often banded, especially in young individuals (various authors).

Habitat.—The species lives on rocky shores and reefs in crevices, under stones and dead coral; also exposed between tides and in shallow water in certain areas (Verrill, 1908). In North Carolina this form is found on offshore reefs and has been found in the sponge *Stematumenia strobilinia* (Lamarck) at Dry Tortugas, Fla. (Pearse, 1934). Intertidal to 30 fathoms.

Type locality.—Guiana.

Known range.—From Cape Hatteras, N.C., through Gulf of Mexico to Rio de Janeiro, Brazil; Bermuda.

Remarks.—Ovigerous females have been taken in Florida from November to February and from June to August; they are known from the Gulf of Mexico in February, Curaçao in April, Barbados and Aruba in midsummer, and from Venezuela in September and November (Rathbun, 1925; U.S. National Museum records). Some of the larval stages have been described by Lebour (1944).

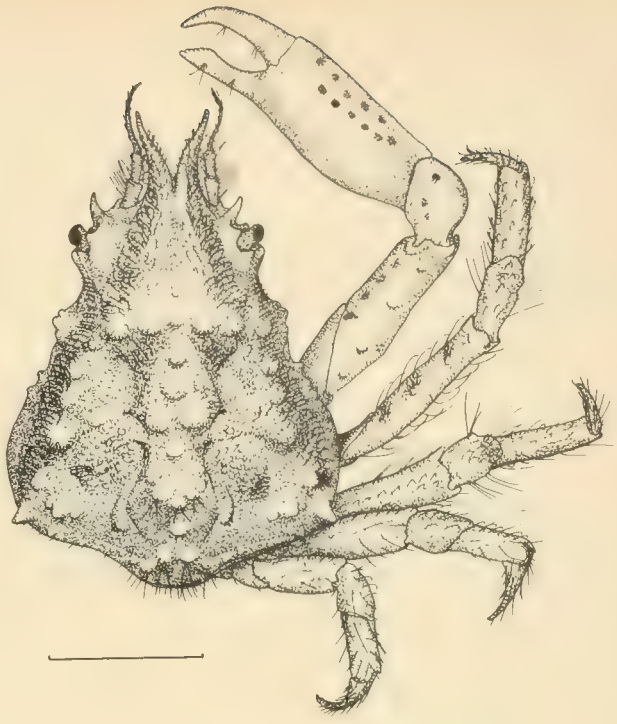

FIGURE 239.—*Microphrys bicornutus* (Latreille). Male in dorsal view, legs of left side not shown, 10 mm. indicated.

Genus *Microphrys* H. Milne Edwards, 1851

Garth, 1958, p. 385.

KEY TO SPECIES IN THE CAROLINAS

a. Carapace without lateral laminiform processes; one strong branchial spine_____*bicornutus* (p. 259).

aa. Carapace with two lateral laminiform processes; two strong branchial spines_____*antillensis* (p. 260).

Microphrys bicornutus (Latreille)

Figures 239, 245F

Pisa bicornuta Latreille, 1825, p. 141.

Microphys bicornutus: Hay and Shore, 1918, p. 459, pl. 38, fig. 10.—Rathbun, 1925, p. 489, text-fig. 139, pl. 175 (rev.).

Recognition characters.—Carapace subtriangular, moderately hairy, all raised parts covered with rounded tubercles; a line of four tubercles arching upward on intestinal region, branchial region with two or three short spines and another spine at lateral angle. Rostrum composed of two stout horns, divergent throughout or divergent at base with extremities curving inward, one-half to one-third length of remainder of carapace. Basal article of antenna with a conspicuous, flat, obtuse spine at anterior angle and behind this a marginal tubercle or a short stout spine in old individuals. Orbits small, circular, with closed fissures, eyes small, preorbital angle rectangular.

Chelipeds spotted, spots persisting for many years in alcohol; merus with three or four tubercles or short, blunt spines above; carpus somewhat nodose; hand smooth; fingers gaping, hollowed out at tips. Walking legs diminishing noticeably in length from first to fourth pair, hairy, margins somewhat rough.

Abdomen of both sexes with seven separate segments.

Measurements.—Carapace: male, length, 36 mm., width, 26 mm.; female, length, 24 mm., width, 20 mm.

Color.—Variable; carapace often dull yellowish brown or bright purplish rose; chelipeds grayish white, covered with small, round, purplish spots.

Habitat.—The species is common on coral reefs. It is often disguised by foreign objects such as sponges, anemones, hydroids, algae, etc., which

became attached to it. Shallow water to 16.5 fathoms.

Type locality.—Nouvelle Hollande.

Known range.—Near Beaufort, N.C., to Cedar Keys, Fla.; Bahamas to Florianopolis, Santa Catarina, Brazil; Bermuda.

Remarks.—Ovigerous females have been reported from March to August in the Caribbean area, and from November to January in the West Indies, Venezuela, and Brazil (Rathbun, 1925; U.S. National Museum records).

Pearse (1932b), working at Dry Tortugas, listed the copepod *Anthiacus intermedius* from the gill lamellae (accidental guest) and a tapeworm plerocercoid, *Rhynchobothrus*, from the viscera, and (*in* Wilson, 1935) reported a few specimens of *Cancrincola jamaicensis* Wilson from the branchial cavity of this crab.

Microphrys antillensis Rathbun

Figures 240, 245G

Microphrys antillensis Rathbun, 1920, p. 20.—1925, p. 498, text-fig. 141, pl. 176, figs. 3–4 (rev.).

Microphrys platysoma: Hay and Shore, 1918, p. 459, pl. 38, fig. 9.

Recognition characters.—Carapace depressed, tuberculate, and granulate, area at inner angle of branchial region finely granulate; intestinal region with four large, equal tubercles. Anterolateral wall with two laminiform processes, one on hepatic, one on branchial region; hepatic process with anterior end acute, projecting outward and occasionally forward in large individuals, sometimes with outward-projecting tubercle at middle of upper edge; a spine between and below level of hepatic and branchial processes; branchial process not rimmed nor sharply defined. Branchial region with three spines, one forming posterolateral angle occasionally doubled. Posterior margin with row of tubercles increasing in size medially. Rostral horns slender, directed forward, about one-sixth length of remainder of carapace. Basal article of antenna with spine at outer angle about half length of rostral spines. Orbits small, circular, with closed fissures; eyes small; preocular spines acute, about half as long as antennal spines.

Merus of chelipeds with dentate and laminate dorsal crest; carpus tuberculate; palm less than twice as long as broad; fingers widely gaping, immovable finger strongly curved downward. Walking legs sparsely hairy and with a few spines and

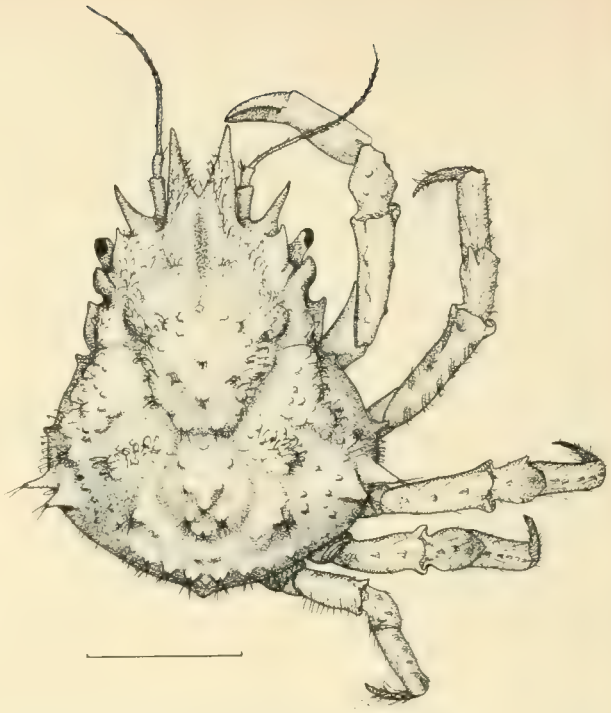

FIGURE 240.—*Microphrys antillensis* Rathbun. Male in dorsal view, legs of left side not shown, 5 mm. indicated.

tubercles; propodi with prominent distal laminiform process for articulation of dactyls.

Abdomen of both sexes with seven free segments.

Measurements.—Carapace: male, length, 18 mm.; width, 16 mm. Length of rostral horns, 3 mm.

Habitat.—Two to 15 fathoms.

Type locality.—Off Montego Bay Point, Jamaica.

Known range.—Beaufort Harbor, N.C., to Cape Fear, N.C.; Cuba; Jamaica; Puerto Rico.

Remarks.—Ovigerous females have been reported in September from North Carolina (Rathbun, 1925), in June from Florida, and November from Bimini (U.S. National Museum records).

Genus ***Stenocionops*** Desmarest, 1823

Garth, 1958, p. 401.

KEY TO SPECIES IN THE CAROLINAS

a. Hepatic region not enlarged nor produced beyond general outline of carapace, armed with not more than one large spine.

b. Marginal spines behind orbit four, carapace with about four median spiniform tubercles
furcata coelata (p. 261).

bb. Marginal spines behind orbit three, carapace with about eight median spines
spinimana (young) (p. 262).

aa. Hepatic region enlarged and produced separately from curve of branchial region, marginal hepatic spines 3; carapace with 12 or 13 median spines
spinimana (adult) (p. 262).

Stenocionops furcata coelata (Milne Edwards)

Figures 241, 245H

Pericera coelata Milne Edwards, 1878, p. 224.
Stenocionops furcata coelata: Hay and Shore, 1918, p. 460, pl. 39, fig. 3.—Rathbun, 1925, p. 540, pl. 164 (rev.).

Recognition characters.—Carapace oblong-ovate, approximately three-fourths as wide as long, uneven, with strong spines and a dense covering of short setae and many scattered, longer, hooked hairs. Rostrum consisting of two nearly straight diverging horns with rows of hooked setae. Orbital region broad, eyes small, retractile within tubular orbits; preorbital spine strong, suborbital and postorbital spines much smaller.

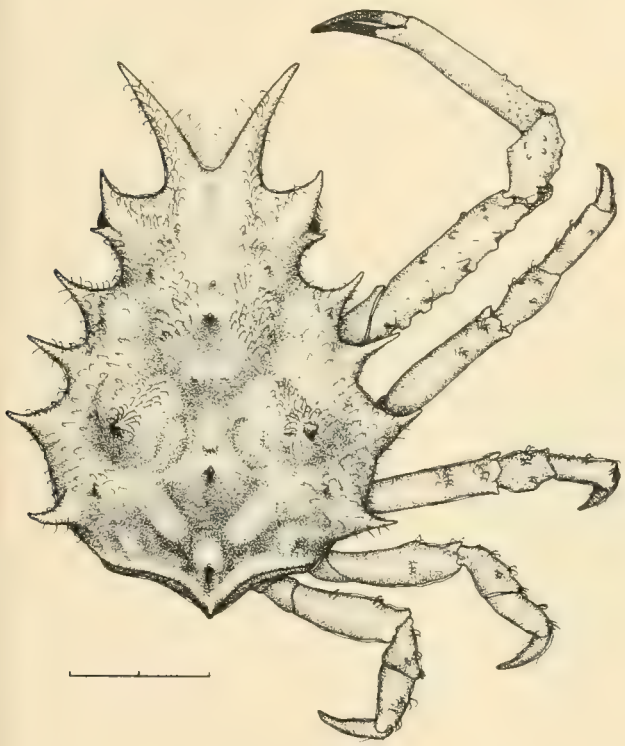

FIGURE 241.—*Stenocionops furcata coelata* (Milne Edwards). Male in dorsal view, legs of right side in part after Rathbun (1925), legs of left side not shown, 20 mm. indicated.

Basal antennal article enlarged, armed with one or two small distal spines or tubercles not visible dorsally. Middorsal line with four strong spiniform tubercles, one on gastric region, remainder on cardiac and intestinal regions, fourth spine with tip curved forward. Lateral border with four stout spines, one on hepatic, remainder on branchial region; in addition, two other stout spines on branchial region and various smaller ones toward front. Ventral surface of body, except distal articles of chelipeds, closely covered with bulbous setae hiding carapace.

Chelipeds in adult males fairly large and nodose; hand long, cylindrical, and granulate; fingers approximately half as long as palm, gaping in basal half, a tooth on dactyl near base. In other individuals chelae weak; fingers less than half as long as palm; merus with strong spines above near distal end preceded by several smaller spines. Walking legs moderately elongate, more or less rough with clusters of hooked hairs, articles subcylindrical.

Abdomen in male and female with seven distinct segments.

Measurements.—Carapace: large male, length, 137 mm.; width, 111 mm. Length rostral horn, 26 mm. Carapace: smaller male, length, 91 mm.; width, 64 mm. Length rostral horn, 25 mm.

Variations.—Large specimens have relatively shorter rostral horns than smaller individuals; young specimens are smoother than old ones.

Color.—Dark red.

Habitat.—This species is found on a variety of bottoms, including fine white sand, yellow sand, coarse gray sand, sand with algae, sandy shell, broken shell, and coral. It has been reported most often from coarse bottom (Rathbun, 1925), and occurs on shelly reefs off Beaufort Inlet, N.C. Shallow water near shore to 60 fathoms, rarely to 278 fathoms.

Type localities.—Ten miles from Jolbos Islands [Yucatan], and near Havana [Cuba], 175 fathoms.

Known range.—Off Beaufort, N.C., to northwest Florida and Alabama; Yucatan Channel; West Indies to Barbados.

Remarks.—This species is similar to the typical subspecies *S. f. furcata* which ranges from Georgia to Bahia, Brazil, in shallow water near shore to 35 fathoms depth. The typical subspecies has the carapace more evenly sculptured and is

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less spinous than *S. f. coelata* (Rathbun, 1925, p. 449).

Ovigerous females are known in Florida from March to August (U.S. National Museum records).

Stenocionops spinimana (Rathbun)

Figures 242, 245I

Libinia spinimana Rathbun, 1892, p. 240, pl. 30.
Stenocionops spinosissima: Hay and Shore, 1918, p. 460, pl. 39, fig. 2.
Stenocionops spinimana: Rathbun, 1925, p. 457, pl. 267 (rev.).

Recognition characters.—Carapace subpyriform, convex, covered with sparse growth of short, fine, curled hairs; 8 to 13 median dorsal spines, and numerous other spines on gastric and branchial regions; anterior marginal hepatic spines 3, anterior-most spine small and occasionally absent in old individuals. Rostral horns widely divergent, straight, tapering gradually to slender tip. Orbits tubular, not strongly projecting, eyes small, retractile within orbits; preorbital spine acute, curving forward slightly at tip; postorbital spine similar in size to spine near anterolateral angle of basal article of antenna.

Merus and carpus of chelipeds with numerous spines, hand rough throughout length with two rows of spines above, one below, spines becoming progressively smaller distally. Walking legs with a few spines. Meral articles with a terminal spine above, and on first leg a longitudinal inner-upper row of five or six, and a ring of about four spines near distal end; on second leg a ring of three or four; on third and fourth only one or two spines besides terminal one. Carpus of first leg with three or four spines, second with three spinules or tubercles, third and fourth with one.

Abdomen in male and female with seven segments, six free in females.

Measurements in millimeters	Large male	Holotype of *spinimana* (male)	Half-grown male	Young female
Length of carapace, including horns	130	89	53	18
Width of carapace, including spines	118	76	42	13
Width of carapace, excluding spines	110	69	36	10
Length of rostral horns	11	10	10	3

Variations.—This species exhibits great change in shape and spination with increasing age, as has

FIGURE 242.—*Stenocionops spinimana* (Rathbun). Holotypic male in dorsal view (after Rathbun, 1892).

been pointed out by Rathbun (1925), and Garth (1958) for related forms. Young individuals are much different in shape from adults, having a width considerably less than length (width about 70 percent of length including spines and rostrum), whereas the mature animals are more rounded in contour (large adult male, with about 90 percent of length). Old individuals have a thicker coating of hair than immature ones, especially on the chelipeds. Chelipeds in old individuals become quite large and stout with the palm compressed (length more than twice that of carapace). The young have fewer spines than adults, the hepatic region is not expanded and bears only one marginal spine as opposed to three spines in adults.

Habitat.—The species has been found on a variety of bottoms, from gray mud, through various grades of sand, to sand-shell, coral, and rock (Rathbun, 1925). Twenty to 124 fathoms.

Type locality.—Off Cape Lookout, N.C., 124 fathoms.

Known range.—Off Cape Hatteras, N.C., to Florida Straits and Gulf of Mexico off Mobile Bay, Ala.

Remarks.—Ovigerous females have been reported from South Carolina in December (Rathbun, 1925).

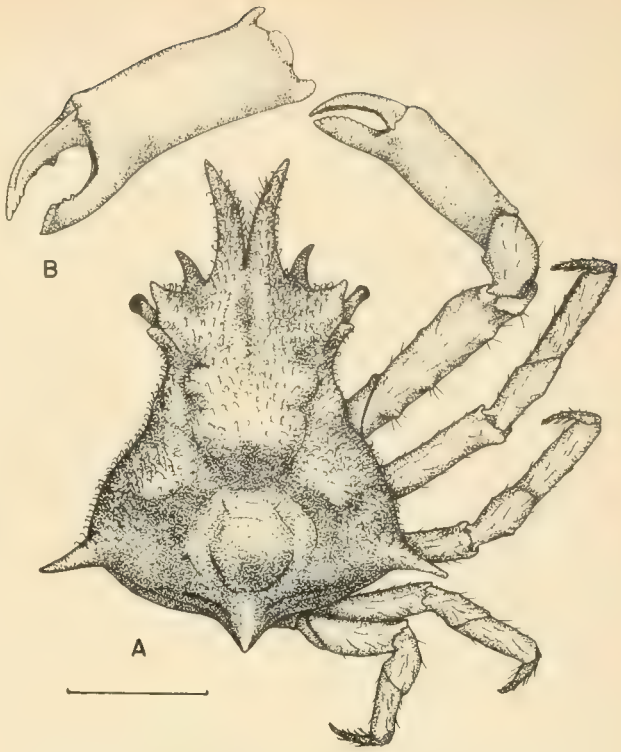


FIGURE 243.—*Macrocoeloma trispinosum* (Latreille). A, small male in dorsal view, legs of left side not shown, 10 mm. indicated; B, right chela of adult male in frontal view.

Genus *Macrocoeloma* Miers, 1879

Garth, 1958, p. 412.

KEY TO SPECIES IN THE CAROLINAS

a. Carapace without dorsal spines in addition to epibranchial and posterior spines____*trispinosum* (p. 263).
aa. Carapace with dorsal spines in addition to epibranchial and posterior spines_____*camptocerum* (p. 264).

Macrocoeloma trispinosum (Latreille). Grass crab, sponge crab, decorator crab

Figures 243, 245J

Pisa trispinosa Latreille, 1825, p. 142.
Macrocoeloma trispinosum: Hay and Shore, 1918, p. 457, pl. 38, fig. 11.—Rathbun, 1925, p. 466, text-fig. 132, pl. 166, fig. 1; pl. 167 (rev.).

Recognition characters.—Carapace irregularly triangular, body and legs with velvety covering of short brown hairs, thick and swollen, wide at level of orbits, narrowing distinctly in hepatic portion, widening again posteriorly. Middorsal region much elevated and bearing four low, rounded tubercles or bosses, one on gastric, one on cardiac, and one on each epibranchial region. Posterolateral angle prolonged into a long flattened spine directed obliquely outward and backward, sometimes curved upward; posterior margin with broad, median, triangular projection with tip sometimes slightly recurved. Rostrum formed of two somewhat flattened horns adjacent and subparallel at base, divergent distally. Eyes retractile within roomy, projecting, tubular orbits, upper margin of orbit deeply emarginate, pre- and post-ocular teeth prominent, preocular teeth curved forward. Basal article of antenna with inner angle produced, exceeding frontal margin, and forming a broad spine directed obliquely outward at each side of rostrum.

Chelipeds of male narrow, approximately as long as carapace; merus nodose; palm with subparallel sides; dactyl approximately half as long as upper margin of palm and lightly furrowed above. Walking legs rather slender, slightly nodose.

Abdomen with seven separate segments in both sexes.

Measurements.—Carapace: male, length, 34 mm.; width, 29 mm.

Variations.—Rathbun (1925) discussed variation in this species throughout its known range. Body shapes falling into three general series are distinguishable. In the first, the typical form, the posterolateral prominences are narrow, with regularly tapering spines, projecting beyond the general outline of the carapace and directed more or less backward, and sometimes strongly curved from base to tip with the concavity forward. The carapace is considerably constricted behind the orbits. The orbits are prominent owing to this constriction, and the pre- and post-ocular teeth are strong, the former directed forward and curved. The upper edge of the orbit is deeply emarginate. The four large tubercles or bosses are prominent, some or all with an acute tip, that on the gastric region sometimes nearly a spine.

In the second series, treated by Rathbun as an unnamed variety, the posterolateral prominences are wider than in the first series, less spinelike and more laminate, their hind margins nearly transverse. The carapace is less narrowed behind the orbits, the orbital teeth less marked, though the preocular tooth is directed forward and a little curved, and the superior emargination less deep. The four large dorsal bosses are lower than in series one, but the gastric boss tends to be surmounted by a sharp tubercle or granule.

In series three, called *M. t. nodipes*, the posterolateral prominences are broader and more obtuse than in series two with their margins almost continuing the margin of the carapace. The carapace is constricted little or not at all behind the orbits; the preocular tooth is acute but not prominent, and the postocular tooth blunt or subacute with both teeth somewhat more prominent in young individuals than in old ones. The orbit has a slight emargination in the upper border. The dorsal bosses are lower than in the other series, smoothly rounded and blunt.

In the three series the posterior median spine varies in a manner similar to the lateral spines. Within the three series, the rostrum shows great variability in length, direction, and curvature of the horns.

Color.—Hairs yellowish or reddish brown (various authors).

Habitat.—In North Carolina, this species has been found in seaweed in Beaufort Harbor, in the ocean on floating masses of *Sargassum*, and dredged from offshore reefs. Elsewhere it has been found in a variety of situations, from pilings and mangrove roots to weedy rocks, coarse-coral sand, sand-shell, and broken-shell bottoms. The species is often concealed by a covering of sponge. Shallow water to 45 fathoms.

Type locality.—Nouvelle Holland (?) [error].

Known range.—Beaufort, N.C., to Alligator Harbor, Fla.; Yucatan; through West Indies to off Cape São Roque, Brazil.

Remarks.—Ovigerous females have been reported from southern Florida in December, Cuba in April, and Jamaica and St. Thomas in July (Rathbun, 1925; U.S. National Museum records).

Macrocoeloma camptocerum (Stimpson)

Figures 244, 245K

Pericera camptocera Stimpson, 1871a, p. 112.
Macrocoeloma campterocerum: Hay and Shore, 1918, p. 457, pl. 38, fig. 12.—Rathbun, 1925, p. 469, pl. 174, fig. 4; pl. 270, fig. 2 (rev.).

Recognition characters.—Carapace irregularly triangular; surface covered with short, close

FIGURE 244.—*Macrocoeloma camptocerum* (Stimpson). Male in dorsal view, legs of left side not shown, 10 mm. indicated.

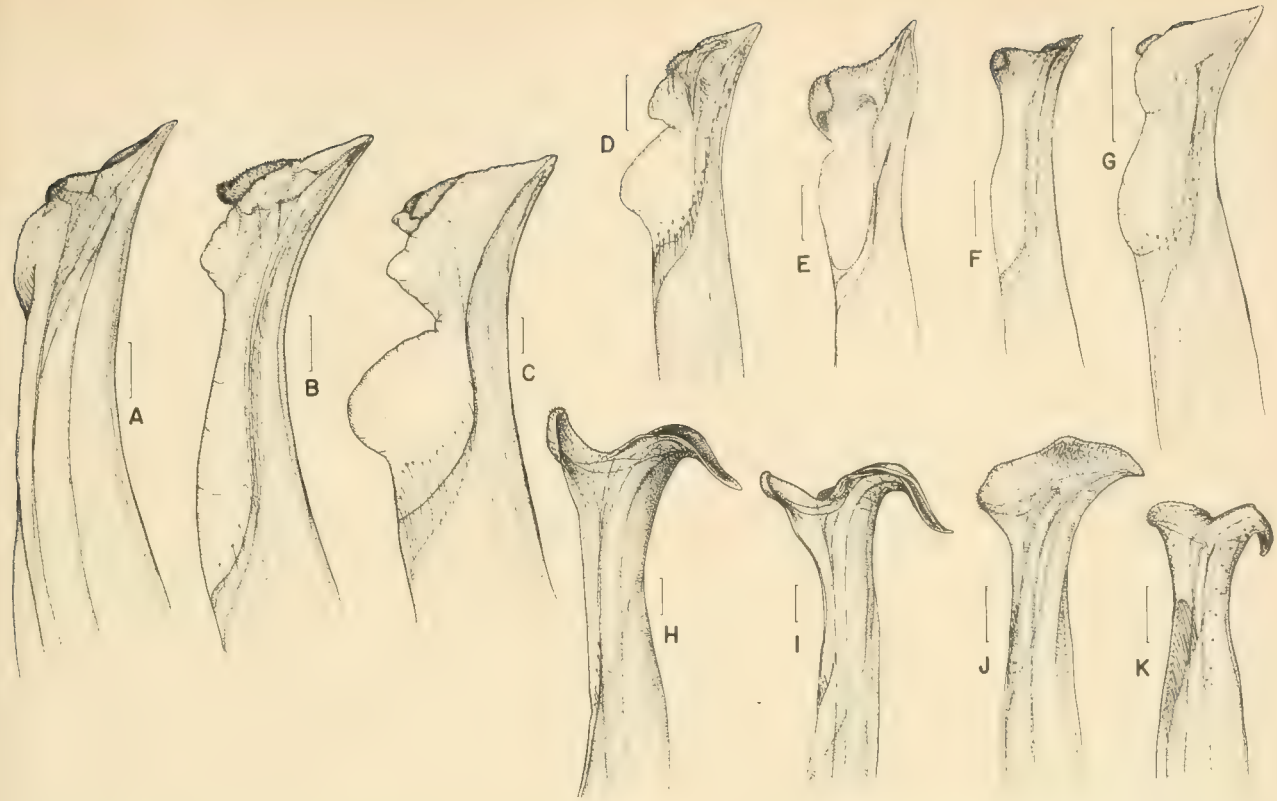


FIGURE 245.—Subfamily Mithracinae, tips of right first pleopods of males; A, *Mithrax spinosissimus* (Lamarck), sternal view; B, *Mithrax verrucosus* H. Milne Edwards, sternal view; C, *Mithrax hispidus* (Herbst), sternal view; D, *Mithrax pleuracanthus* Stimpson, sternal view; E, *Mithrax forceps* (Milne Edwards), sternal view; F, *Microphrys bicornutus* (Latreille), sternal view; G, *Microphrys antillensis* Rathbun, sternal view; H, *Stenocionops furcata coelata* (Milne Edwards), sternal view; I, *Stenocionops spinimana* (Rathbun), sternal view; J, *Macrocoeloma trispinosum* (Latreille), lateral view; K, *Macrocoeloma camptocerum* (Stimpson), lateral view; 0.33 mm. indicated.

pubescence, and, in addition, long, stiff, curled hairs on front, gastric region, and lateral portions of branchial regions; wide at level of orbits, narrowing distinctly in hepatic portion, widening again posteriorly; with four strong spines on dorsal region, one on gastric, one on cardiac, and one on each epibranchial region. Posterolateral spines subconical, regularly tapering, acute, and directed slightly backward; posterior median spine shorter, acute, obliquely erect. Rostral horns acute, rather regularly divergent from base. Spines on basal article of antennae rather slender, divergent. Orbital tubes, pre- and post-orbital spines protuberant laterally, preorbital spine curving a little forward.

Chelipeds of male strong, longer than carapace; merus with a few short spinules above; carpus somewhat nodose with a tubercle at inner angle; palm widest near articulation; fingers tipped with black or dark brown. Walking legs nearly smooth.

Abdomen with seven separate segments in both sexes.

Measurements.—Carapace: male, length, 40 mm., width, 36 mm.; female, length, 24 mm., width, 20 mm.

Variations.—The rostral horns may be straight or slightly curved outward at tips, and range in length from one-sixth to one-third the total length of the carapace. The interspace between horns may vary from a narrow V-shape to almost a right angle. The posterolateral spine may be straight in frontal section or curved upward and nearly transverse or directed strongly backward.

Color.—A dirty brown.

Habitat.—The species has been taken on a variety of bottoms ranging from sand with grass, or a hard smooth substrate, to rocky or coral bottoms. Rathbun (1925) reported the form from predominantly coarse bottoms. About 2 to 13 fathoms.

Type locality.—Near Key West [Fla.], in from 2 to 5 fathoms.

Known range.—Beaufort Harbor, N.C., via southern Florida to Alligator Harbor, Fla.

Remarks.—Ovigerous females are known in Florida from January to March (U.S. National Museum records).

Family **Parthenopidae**

Eyes usually retractile within small, circular, well-defined orbits, floor of orbit nearly continued to front, leaving a hiatus usually filled by second [article] of antennary peduncle. Basal antennal [article] small, deeply imbedded between inner angle of orbit and antennulary fossae. Antennules folding somewhat obliquely (Alcock, 1895).

Subfamily **Parthenopinae**

Carapace commonly equilaterally triangular, sometimes subpentagonal or ovate-pentagonal, and sometimes almost semicircular or semielliptical in outline. Cardiac and gastric regions usually deeply marked off from branchial regions on either side, making dorsal surface of carapace trilobed. Rostrum simple or obscurely trilobed. Chelipeds vastly longer and more massive than walking legs (Alcock, 1895). First pleopod varying, more or less stout, apically tapering or not tapering; second pleopod usually short and of usual shape (Stephensen, 1945).

KEY TO GENERA IN THE CAROLINAS

(Modified after Rathbun, 1925)

a. Carapace not laterally expanded over walking legs.
  b. Carapace tuberculate or eroded.....*Parthenope* (p. 266).
  bb. Carapace smooth, except for a few strong spines.....*Solenolambrus* (p. 270).
aa. Carapace more or less expanded forming a vault beneath which walking legs are concealed.....*Heterocrypta* (p. 270).

Genus ***Parthenope*** Weber, 1795

Garth, 1958, p. 434.

KEY TO SPECIES IN THE CAROLINAS

a. Carapace ovate-pentagonal, surface scarcely carinate in adult (Subgenus *Parthenope*).....*agona* (p. 266).
aa. Carapace broadly triangular, carinate or tuberculate, with more or less rounded sides (Subgenus *Platylambrus*).
  b. Carapace and chelipeds very flat; spine at end of main dorsal branchial ridge small.....*serrata* (p. 267).
  bb. Carapace convex, chelipeds not flat; spine at end of main dorsal branchial ridge large.
    c. Carapace much broader than long; hand with 8-12 teeth on inner, 10-12 on outer margin.....*pourtalesii* (p. 268).
    cc. Carapace not much, if any, broader than long; hand with few good sized marginal teeth, six to eight on inner, three to five on outer margin.....*fraterculus* (p. 269).

Parthenope (Parthenope) agona (Stimpson)

Figures 246, 252A

Lambrus agonus Stimpson, 1871a, p. 131.
Parthenope agona: Hay and Shore, 1918, p. 462, pl. 39, fig. 5.
Parthenope agonus: Rathbun, 1925, p. 513, text-fig. 146, pls. 178–179; pl. 275, figs. 1–3 (rev.).

Recognition characters.—Carapace ovate-pentagonal or subcircular, somewhat broader than long, with rounded sides, without angles. Postorbital constriction slight, not involving pterygostomian ridge continuing from lower side of orbit to point above cheliped. Depressions be-

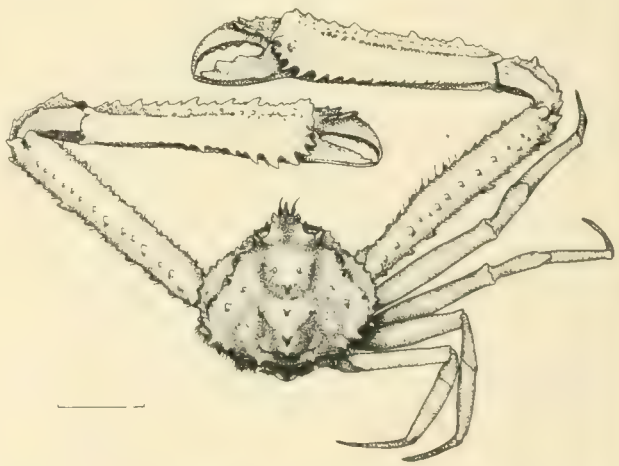


FIGURE 246.—*Parthenope (Parthenope) agona* (Stimpson). Male in dorsal view, position of legs reconstructed, walking legs of left side not shown, 10 mm. indicated.

tween regions of carapace not markedly deep; surface coarsely punctate or eroded, and with numerous granules and tubercles, larger tubercles more or less spiniform and arranged as follows: five on gastric region, three on cardiac, one on each side of urocardiac lobe, five on branchial, and one on each hepatic region. Anterolateral margin of branchial region with six small teeth, below and behind last tooth a broad triangular tooth, and still lower on ventral surface a spine visible between ischia of cheliped and first leg. Median rostral tooth narrow, produced, denticulate at base, an acute forward-pointing tooth over each antennular cavity. Orbit with several spines on outer margin, a suture above, open below; eye with small spine on upper surface. A conical spine or tubercle on each side of sternum near base of chelipeds.

Chelipeds long, slender (length of merus approximately 1.3 times width of carapace), prismatic, upper surface finely rugose. Merus and carpus with an irregular row of dentiform tubercles near middle of upper surface, on inner and outer margins, and near outer margin of hand. Upper margin of hand with row of 18–20 irregular teeth, largest near base of fingers but decreasing in size both proximally and distally; outer margin with 4 to 6 larger teeth and many intermediate smaller ones. Walking legs long, slender, bare, and almost smooth.

Second segment of abdomen with sharp transverse crest.

Measurements.—Carapace: male, length, 20 mm.; width, 21 mm. Length of merus, 30 mm.

Variations.—The rostrum may be broadly triangular, subentire, instead of tridentate with denticulate margins. In young individuals the pterygostomian ridge is less developed anteriorly, and the postorbital constriction is more evident.

Color.—Light buff, somewhat marbled with purple, chelipeds and legs with broad bands of purple.

Habitat.—The species has been reported from predominantly sandy or broken-shell bottom (Rathbun, 1925); 25 to 115 fathoms.

Type localities.—Off the Marquesas, Carysfort Reef, and Conch Reef, 40 and 49 fathoms [southern Florida].

Known range.—Off Capes Hatteras and Lookout, N.C.; Gulf of Mexico near Pensacola, Fla., through Florida Straits; Puerto Rico; Trinidad; between British and Dutch Guiana.

Remarks.—Ovigerous females have been taken from southwestern Florida in March (Rathbun, 1925), and off the Guianas in September (U.S. National Museum records).

Parthenope (Platylambrus) serrata (H. Milne Edwards)

Figures 247, 252B

Lambrus serratus H. Milne Edwards, 1834, p. 357.
Platylambrus serratus: Hay and Shore, 1918, p. 463, pl. 39, fig. 7.
Parthenope serrata: Rathbun, 1925, p. 516, pls. 180–181; pl. 275, figs. 7–10 (rev.).

Recognition characters.—Carapace depressed, width approximately 1.5 times length; convex anterolateral margin of branchial region with seven to nine triangular teeth in front of long, flat, lateral spine. Posterolateral margin concave; posterior margin convex, wide, both margins together with seven tubercles noticeably larger than others, each terminating an indefinite longitudinal or oblique line of tubercles. Elevations of carapace ornamented with numerous unequal granulated tubercles; depression between gastric and branchial regions deep. Rostrum short, tridentate, narrow at tip, and with raised margin continuous with superior wall of orbits. Pterygostomian and subhepatic regions with an excavation reaching margin of orbit and, with chelipeds retracted, forming covered efferent passages.

Chelipeds, when extended, approximately 2 to 2.5 times as long as carapace, trigonal, smooth beneath, more or less tuberculate on upper sur-

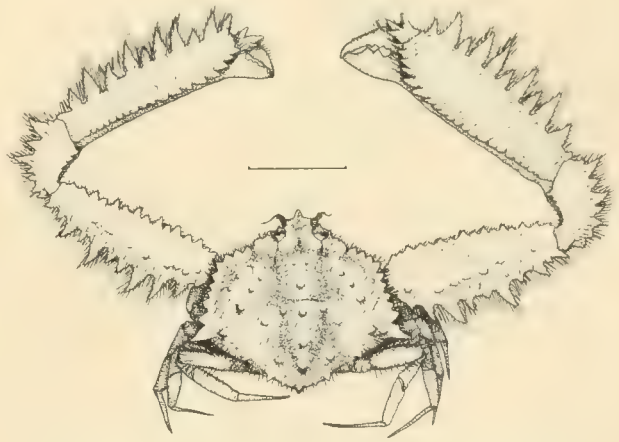


FIGURE 247.—*Parthenope (Platylambrus) serrrata* (H. Milne Edwards). Male in dorsal view, 10 mm. indicated.

face, and with margins cut into lanceolate or triangular teeth fringed with fine hairs, much stronger on outer than on inner side of articles; hand with about nine teeth alternately large and small; fingers stout, oblique. Walking legs of moderate size, longest not exceeding merus of cheliped.

Abdomen of male with segments three to five fused, sixth segment with a median spine.

Measurements.—Carapace: male, length, 19 mm.; width, 28 mm. Length of cheliped, 60 mm.

Color.—Red somewhat mottled with gray; fingers carmine, shading to black.

Habitat.—The species has been reported from a variety of bottoms ranging from coral to fine sand and mud, but it has been taken most often from muddy or sandy bottoms (Rathbun, 1925; Holthuis, 1959). Shallow water to 60 fathoms.

Type locality.—l'Ocean indien [erroneous locality].

Known range.—Off the three North Carolina capes, Gulf of Mexico from Pensacola to southern Florida, and off Campeche, Mexico; West Indies to Bahia, Brazil.

Remarks.—Hildebrand (1955) and Holthuis (1959) added distributional extensions to Campeche and Surinam. Ovigerous females have been reported in May and June from Surinam (Holthuis, 1959). They are known from North Carolina in June, Florida in summer, and Cuba in October (U.S. National Museum records).

Parthenope (Platylambrus) pourtalesii (Stimpson)

Figures 248, 252C

Lambrus pourtalesii Stimpson, 1871a, p. 129.
Parthenope pourtalesii: Hay and Shore, 1918, p. 462, pl. 39, fig. 6.—Rathbun, 1925, p. 521, pls. 182, 183, and 276 (rev.).

Recognition characters.—Carapace broadly ovate-triangular, convex; branchial regions rather deeply separated from gastric, cardiac, and hepatic regions. Posterolateral angle marked by conspicuous laciniated spine located behind bulging curve of anterolateral margin; hepatic margin armed with a small but prominent spine. Anterolateral margin behind cervical suture armed with eight or nine teeth and spines, first three or four shorter than remainder. Posterolateral margin with three or four unequal spines in addition to large one on ridge; posterior margin with three large and several small spines. General surface of carapace pitted and eroded,

FIGURE 248.—*Parthenope* (*Platylambrus*) *pourtalesii* (Stimpson). Female in dorsal view, approximately × 0.80 (after Smith, 1887).

with granulated tubercles disposed as follows: one gastric, one genital, two cardiac, two on branchial ridge in line with lateral spine, and a tendency to rows of tubercles on branchial regions. Rostrum with a long, narrow, obtuse tooth with a denticle on each side, a subacute basal tooth, and below and outside this a short spine. Supraorbital spine blunt, postorbital spine smaller but somewhat sharper; upper side of emargination on eye spined.

Chelipeds long, rough, armed with laciniated teeth and spines on both margins; merus with an additional median row of spiniform tubercles on upper surface; carpus with largest spine at inner angle; hand with an obsolete median row beneath. Meri of walking legs spinulose, also carpus and propodus of last pair; dactyls furred; a tubercle on sternum at base of cheliped and each of legs one to three.

Abdomen with a large tubercle in middle of second to sixth abdominal segments and a conical tubercle at extremity of segments two and three; segments three to five fused in male. Lower surface of body granulate and tuberculate.

Measurements.—Carapace: male, length, 36 mm.; width, 47 mm. Length of cheliped, 122 mm. Carapace: ovigerous female, length, 11 mm.; width, 13 mm.

Variations.—The species varies greatly in the number and prominence of tubercles and teeth, and in constriction and ornamentation of the rostrum. The elevations of the carapace may bear spines or tubercles.

Color.—Purplish red with cross bands of buff on chelipeds and walking legs; palms pinkish brown (various authors).

Habitat.—The species is found predominantly on sand or sandy mud bottoms (Rathbun, 1925); 10 to 134 fathoms.

Type localities.—Off Conch Reef, French Reef, and American Shoal [southern Florida].

Known range.—Off Marthas Vineyard, Mass.; latitude of New Jersey through West Indies to Grenada.

Remarks.—Ovigerous females are known from North Carolina in December.

Parthenope (Platylambrus) fraterculus (Stimpson)

Figures 249, 252D

Lambrus fraterculus Stimpson, 1871a, p. 130.
Parthenope fraterculus: Rathbun, 1925, p. 525, pls. 186–187; pl. 190, fig. 2 (rev.).

Recognition characters.—Carapace subtriangular, approximately four sided, posterolateral margins continuous with sides of posterior margin, and long anterolateral margins in line with rostral borders. Depressions separating branchial from cardiac and hepatic regions deep; cardiac and gastric regions connected by a narrow ridge, hepatic and branchial regions by a wider ridge bounded below by a deep hollow visible in side view; hepatic region with a large submarginal tubercle visible in dorsal view. Margin of branchial region cut into 11 to 13 small teeth; posterior margin with 3 equal teeth. Prominences of carapace ornamented with a few large tubercles and spines as follows: three gastric in a triangle, one genital, two cardiac, and three on branchial ridge. Front inclined about 45 degrees, ending in a narrow, blunt tooth, a blunt tooth on each side above antennules, and outside, below these, a small slender spine. A tubercle on preorbital lobe; orbit with a small blunt tooth on inner lower angle and a large tubercle between this and angle of buccal cavity. Endognath with row of five tubercles near outer margin.

FIGURE 249.—*Parthenope* (*Platylambrus*) *fraterculus* (Stimpson). Male in dorsal view, position of legs reconstructed, legs of left side not shown, 5 mm. indicated.

Chelipeds of male approximately 2.5 times as long as carapace; inner, outer, and upper margins of merus with a few unequal stout spines; inner and outer margin of hand armed with triangular, denticulate, unequal teeth, six or seven larger ones on inner, three or four on outer margin; largest tubercle on upper surface at proximal third conical. Walking legs with meri denticulate; dactyls furred except at tip; carpus and propodus of last pair with two or three lobes above and five denticles below.

Sternum and abdomen tuberculate, second to sixth abdominal segment with a large transverse tubercle.

Measurements.—Carapace: male, length, 16 mm., width, 17 mm.; female, length, 16 mm., width, 18 mm.

Variations.—There is great individual variation in the nature of tubercles and spines. In some individuals the prominences are low and blunt, in others high and sharp. The front may vary in degree of inclination, and margins of the frontal lobes and orbits may be denticulate, entire or subentire.

Color.—Uniform red, eggs bright red (various authors).

Habitat.—The species has been taken predominantly on rocky or shelly bottoms (Rathbun, 1925; Holthuis, 1959); 4 to 110 fathoms.

Type localities.—Off Sand Key, Carysfort and Conch Reefs, West of Tortugas, 26 to 68 fathoms [southern Florida].

Known range.—Off Cape Fear, N.C.; Gulf of Mexico, off Cape San Blas, Fla., to Florida Straits; off Cape Catoche, Yucatan, Mexico; through West Indies to mouth of Amazon River (U.S. National Museum records).

Remarks.—Ovigerous females have been reported in May from southern Florida (Rathbun, 1925), and August from northeastern Florida (U.S. National Museum records).

Genus ***Solenolambrus*** Stimpson, 1871

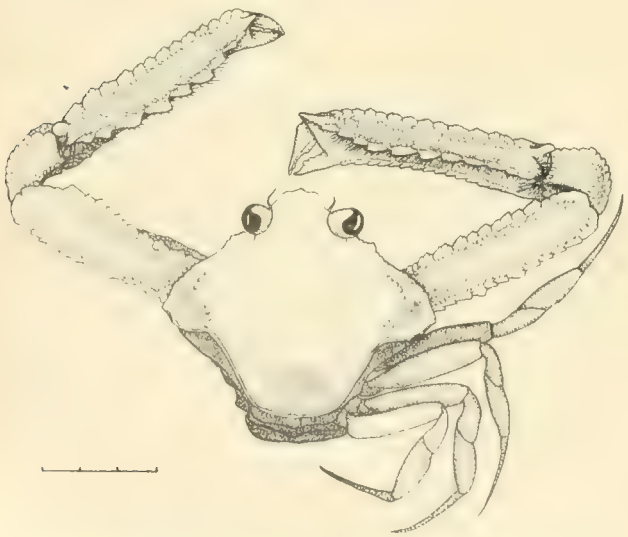
Garth, 1958, p. 458.

Solenolambrus tenellus Stimpson

Figure 250

Solenolambrus tenellus Stimpson, 1871a, p. 134.—Hay and Shore, 1918, p. 463, pl. 39, fig. 8.—Rathbun, 1925, p. 541, pl. 194, figs. 3–4; pl. 279, figs. 5–9 (rev.).

Recognition characters.—Small delicate species. Carapace but little broader than long and about equally produced in front of and behind line of lateral angles; surface punctate; protuberances of gastric and cardiac regions fairly well marked near posterolateral margin but almost obsolete anteriorly. Anterolateral margins of carapace crenulated, five or six teeth on expanded and broadly rounded lateral angle being most prominent and defined chiefly by impressed lines on marginal shelf; hepatic region with two or three denticulate teeth. Posterolateral margin concave; posterior margin convex, its lateral angles obtuse.



250. *Solenolambrus tenellus* Stimpson. Female [illegible] view, walking legs of left side not shown. [illegible]

Rostrum rather prominent, faintly tridentate at extremity, median tooth smallest and most prominent. External angle of orbit not prominent; eyes large with extremely minute tubercle at summit. Basal article of antenna approximately as long as next article. External maxilliped with ischium somewhat tuberculate near outer margin and extremity.

Chelipeds long, slender, general surface smooth, polished; edges denticulate. Merus with about 13 teeth on either edge, third tooth from distal end larger than others. Hand with 12 sharp forward-curving teeth on superior edge, terminal tooth above finger spiniform and considerably longer than others; outer margin with about 11 small teeth, inner with 19 or 20 minute teeth. Walking legs naked, compressed, without laminiform crests; merus of last pair slightly expanded below near base.

Abdomen and sternum of male coarsely pitted, otherwise smooth and glabrous.

Measurements.—Carapace: male, length, 6 mm.; width, 6 mm. Length of cheliped, 16 mm. Carapace: ovigerous female, length, 5 mm.; width, 6 mm.

Habitat.—Thirty to 115 fathoms.

Type localities.—Off Carysfort, Conch, and French Reefs, 35 to 49 fathoms [southern Florida].

Known range.—Off Cape Lookout, N.C.; Gulf of Mexico, near Cape St. George, Fla., to Florida Keys; Bahamas; Barbados.

Remarks.—Ovigerous females have been reported in May from Barbados, May and June from Florida (Rathbun, 1925), and questionably in August from North Carolina (an incompletely labeled specimen from Hay and Shore's material in Institute of Fisheries Research collection, and *Fish Hawk* records for 1902).

Genus ***Heterocrypta*** Stimpson, 1871

Garth, 1958, p. 473.

Heterocrypta granulata (Gibbes). Pentagon crab

Figures 251, 252E

Cryptopodia granulata Gibbes, 1850, p. 173.
Heterocrypta granulata: Hay and Shore, 1918, p. 464, pl. 39, fig. 9.—Rathbun, 1925, p. 555, text-fig. 152, pl. 203, figs. 1–2; pl. 282, figs. 1–3 (rev.).

Recognition characters.—Carapace subtriangular, with wide clypeiform vaulted expansions, length two-thirds width; general surface smooth,

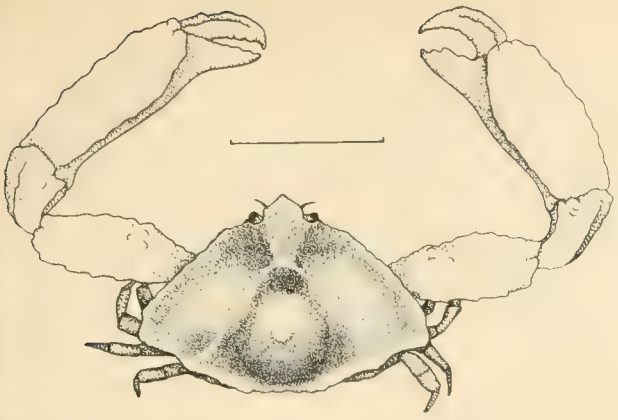


FIGURE 251.—*Heterocrypta granulata* (Gibbes). Male in dorsal view, 10 mm. indicated.

punctate; margins crenulate. Anterolateral margin nearly straight, with dorsal surface sloping upward from margin to prominent, granulate branchial ridge running parallel with each side, these connected by a short transverse ridge on gastric region and joined behind to posterior marginal ridge. Rostrum broad, blunt, deflexed, with rounded margins connected to gastric ridge by a pair of granulate crests. Orbits small, nearly circular; eyes small, retractile. Cardiac region with a large domelike elevation granulated at summit.

Chelipeds unequal, rather heavy, longer than width of carapace; outer and inner margins of upper surface of merus, carpus, and hand expanded into irregular granulate or dentate crests; fingers short, agape in larger cheliped. Walking legs short, almost completely hidden beneath carapace.

Sternum and lower surface of abdomen coarsely granulate; male abdomen with third, fourth, and fifth segments fused, sixth segment with a sharp proximal appressed spine with tip lying between two tubercles on fifth segment.

Measurements.—Carapace: male, length, 12 mm., width, 18 mm.; female, length, 15 mm., width, 21 mm.

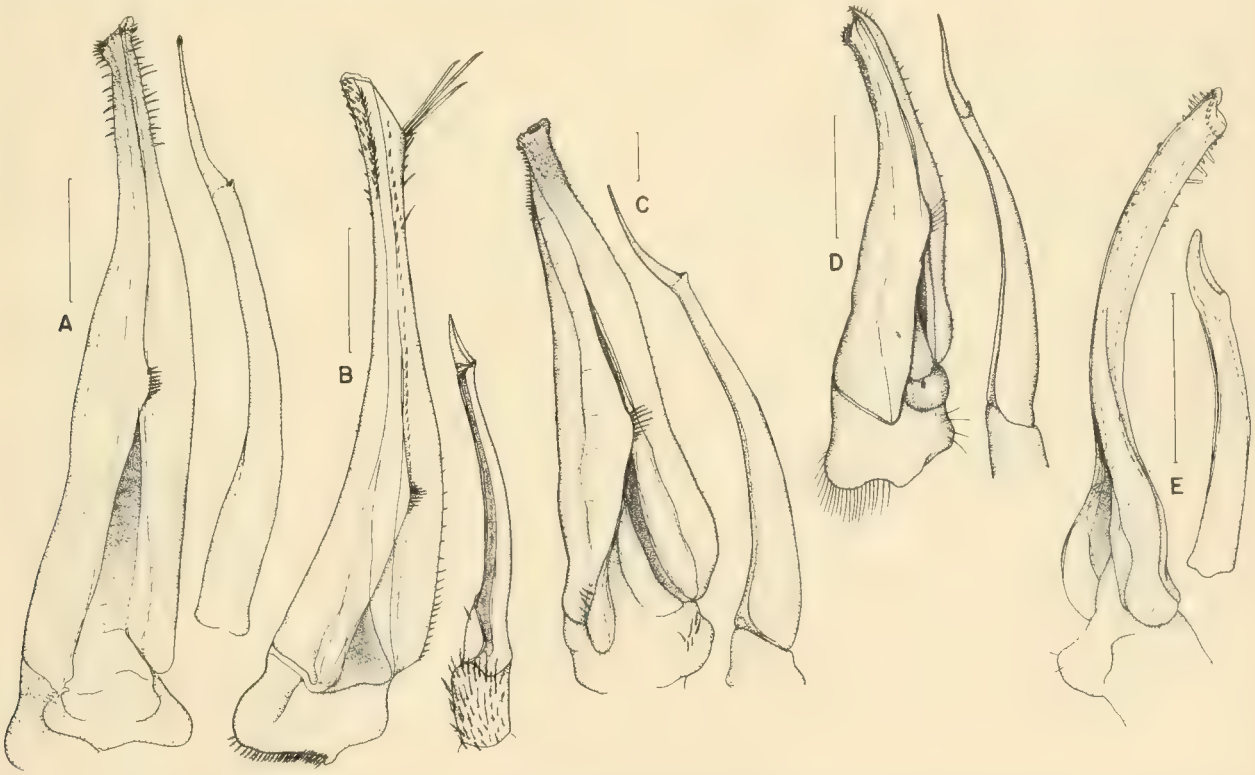


FIGURE 252.—Family Parthenopidae, first and second right pleopods of males; A, *Parthenope agona* (Stimpson), medial view; B, *Parthenope serrata* (H. Milne Edwards), medial view; C, *Parthenope pourtalesii* (Stimpson), medial view; D, *Parthenope fraterculus* (Stimpson), medial view; E, *Heterocrypta granulata* (Gibbes), mediosternal view; 1 mm. indicated.

Color.—Varying from light gray to nearly black, usually commingled so as to produce an irregular mottling or marbling (various authors).

Habitat.—This species is found on shingly bottoms, and not infrequently on shelly bottoms in Morehead City, N.C., harbor. Its angular form and coloration bear so close a resemblance to fragments of shells among which it lives that it is extremely difficult to detect. Two to 75 fathoms.

Type localities.—Near Kiawah Island, Sullivans Island, and White Point Shoal, Charleston Harbor, S.C.

Known range.—Nantucket Sound, Mass., to Georgia; Florida Straits to Sabine, Tex.; through West Indies to St. Thomas.

Remarks.—Ovigerous females are found in the Beaufort, N.C., area throughout the summer.

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ANNUAL MARKS ON SHELL AND LIGAMENT OF SEA SCALLOP (*PLACOPECTEN MAGELLANICUS*)

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ABSTRACT

The annual rings on the shell of the sea scallop are frequently weak or obscured by other rings caused by some nonannual stress. Methods are presented by which it is possible to locate the true annual rings by reference to marks on the resilium, changes in shell curvature, changes in color pattern, weight of the shell, and areas of attack by boring organisms. The results obtained are validated by comparing a growth rate derived through location of the annual rings with one derived from the growth increments of a large sample which had been tagged and released and recaptured after a year at large. The objectivity of the criteria used to identify the annual rings was tested.

ANNUAL MARKS

Many investigators have been able to determine the growth rate of various species of mollusks by identifying those rings on the shell that are caused by some consistent annual phenomenon. Measuring the amount of shell between the rings provides data from which it is possible to estimate growth rates for various areas and year classes. Canadian investigators (Stevenson and Dickie, 1954; Dickie, 1955) succeeded in applying this technique to the sea scallop, *Placopecten magellanicus* (Gmelin), of the Bay of Fundy. Dickie (personal communication) also succeeded, with some difficulty, in locating annual rings on the sea scallops of Georges Bank. His difficulty was caused by the fact that the annual rings are usually rather weak and frequently masked by the presence of strong shock rings. Sea scallops are rather sensitive creatures, and any serious disturbance causes them to mark the event with a shock ring on the shell (Posgay, 1950). The grounds that interest us most are those on Georges Bank, which sustain the heaviest fishing pressure and where concentrated dredging operations may cause uncaught scallops to form many shock rings (fig. 1).

Because of the difficulties of interpreting the rings on the shell, we have examined some of the other hard parts of the sea scallop for characteristics that might offer clues to age. The most useful of these structures proved to be the calcareous part of the resilium. Areas attacked by boring organisms, weight of the shell, color changes, and changes in the curvature of the shell also provided valuable clues to age.

This paper describes the methods used to determine the position of the annual rings, gives the result of applying them to a sample of shells, compares the derived growth rate with the growth rate determined from tagged and recaptured animals, and gives the result of an experiment testing the objectivity of the criteria. Each phase of the work was carried out by a different investigator to avoid subjective bias.

RINGS ON THE SHELL

The surface of the shell of the sea scallop is covered with a series of fine concentric lines (circuli) as a result of the addition of new shell along the margin during growth. At intervals,

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FIGURE 1.—Upper valve of sea scallop showing strong shock rings and weak annual rings.

the circuli are more closely spaced and give the appearance of a band or ring (fig. 2). These bands are laid down annually as the result of a decrease in the rate of growth much as has been demonstrated for tree rings and fish scales. Although the cause has not yet been demonstrated, we believe that it is low winter temperatures. Specimens from shallow water (fig. 3), where winters are more severe, have more prominent rings than those from deeper water where temperatures vary less. Georges Bank, with an average annual temperature range of 8°–12° C., has a particularly equable climate for sea scallops. Posgay (1953) has shown that sea scallops grow fastest at about 10° C. In his experiments, the rate dropped to about 95 percent of the maximum at 8° C. and to about 80 percent at 12° C.

In addition to the annual rings, most sea scallop shells exhibit other annuli which mark nonannual

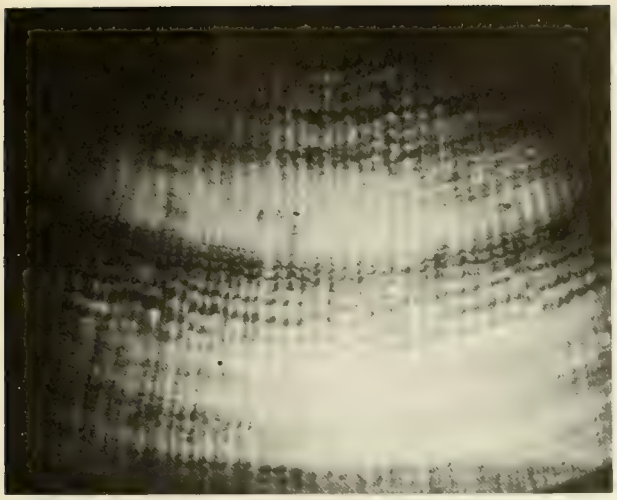

FIGURE 2.—Closeup view of a portion of the upper valve of a sea scallop, showing a band of narrowly spaced circuli between two areas of widely spaced circuli.

phenomena. In shallow water, a severe storm may cause sufficient disturbance on the bottom to cause the scallops to form shock rings. Offshore, shock rings are usually caused by dredging activities of the fishing fleet. Lightly fished areas yield unmarked scallops, while heavily fished areas yield scallops whose shells are a confusion of shock rings. These injuries are sometimes so severe as to distort the shape of the shell (fig. 4).

On Georges Bank, which provides more than 75 percent of the sea scallop catch, both phenomena, weak annual rings and many shock rings, combine to make the location of the annual rings difficult (fig. 1). Not all scallops, however, react in the same degree to the stress that causes the annual ring. Any reasonably large sample will contain some sensitive individuals bearing clear annual rings. Likewise, not all scallops are subjected to disturbances sufficient to cause many shock rings. It is usually possible, therefore, to sort out at least a few shells which are fairly easy to interpret. While such a small sample of selected individuals cannot give a valid estimate of the growth rate of the population, it can give an idea of what to expect from the rest of the sample. The more deeply curved valve, which is uppermost when the scallop is at rest, usually bears the clearest annual rings; but in some individuals, the lower valve will be more easily interpreted.

MARKS ON THE LIGAMENT

The structure and the function of the ligament in *Pecten* have been fully described by Trueman (1953a, and 1953b). The outer layer (fig. 5) unites the two valves and acts as a flexible hinge. The inner layer, the resilium, is composed of a large, dark-brown, conical, central structure of rubbery, noncalcareous material and two small lateral calcareous plates, which cement the resilium into a shallow socket, the resilifer, on each valve. The resilium acts as a sort of compressible spring working in opposition to the adductor muscle. When the muscle is relaxed, the resilium forces the margins of the valves apart.

As the scallop grows and adds new shell along the margins, it also adds new material to the ligament. When shell growth slows or ceases, ligament growth also slows or ceases producing a mark. The resilium, and the epithelial cells which produce it are well protected and less exposed to shock and injury than are the margins of the shell and the cells which produce it. Therefore, marks on the resilium caused by an annual period of slow growth are relatively more prominent compared with shock marks than are the corresponding marks on the shell. The spaces between the bands on the resilium are proportional to the spaces between the bands on the shell; hence, a specific area of the resilium can be referred to a corresponding part of the shell. This section of the shell can then be studied closely in search of the annual ring.

Figure 6 shows the upper valve of a sea scallop, selected because of its distinct annual rings and lack of strong shock rings, which has been sawed down the midline. The numbers indicate annual rings. Figure 7 shows the resulting cross section of the hinge area of the same scallop. The dark area in the center of the cross section is the resilium; the lighter areas immediately to the left and right are the calcareous plates. The numbered, darker bands on the plates and the constrictions of the resilium correspond to the five annual rings on the shell.

It is not necessary to make a cross section in order to observe the annual marks on the plates of the resilium. When the valves of a sea scallop are separated, the resilium usually splits down the middle. After drying for a few days, the remaining half of the resilium, including the attached

FIGURE 3.—Upper valve of a sea scallop taken from shallow water showing prominent annual rings.

calcareous plate, can be easily picked out of the resilifer. The plate can then be examined with a low-power microscope or hand lens (fig. 8). If the ligament has been lost, it is still possible to examine the corresponding impression on the resilifer.

OTHER SHELL CHARACTERISTICS

In some areas, annual invasions of boring organisms infect the upper valve of the sea scallop (figs. 6 and 9). The areas of heaviest infestation can be easily seen if the shell is held over a strong light. The annual rings can usually be located between the infected areas. The weight of the shell is sometimes an index of rate of growth. A thin shell is usually the sign of a fast growing individual; a thick, heavy shell usually means slow growth. Some shells exhibit areas of convex curvature between the annual rings (fig. 10). The profile of these shells, held at arm's length, show a series of hills and valleys. The annual rings can usually be found in the valleys. An occasional shell, or sample of shells from particular areas, will show changes in color pattern of an annual

FIGURE 4.—Upper valve of a sea scallop taken from a heavily fished area, showing malformation as a result of injury to the mantle.

nature which may help to locate the rings (fig. 11). Figures 9, 10, and 11 represent selected individuals; obviously, not all shells are so strikingly marked.

READING A SAMPLE

The shells to be read must first be cleaned of all foreign matter. It is best to soak them in a strong solution of a nonbleaching detergent and then scrub them with a wire brush. The length frequency is determined to see if the sample is polymodal. We define length for these purposes as being measured along the greatest diameter of the shell from umbo to opposite margin. Shells that do not have a large number of shock rings and appear to have prominent annual rings are then sorted out. The shells and resilia of these individuals are studied first, and a preliminary table of length at time of annual ring formation is prepared.

With this table as a guide to the most probable location of the annual rings the rest of the sample is read. It is best to work from the smaller to the larger specimens. All of the clues mentioned previously are used as occasion demands and opportunity affords. The more difficult shells are set aside until the last when the averages and the deviations are more firmly established. These, as well as the larger, older shells with the annual rings near the margin crowded together, can usually be best interpreted by reference to the resilia.

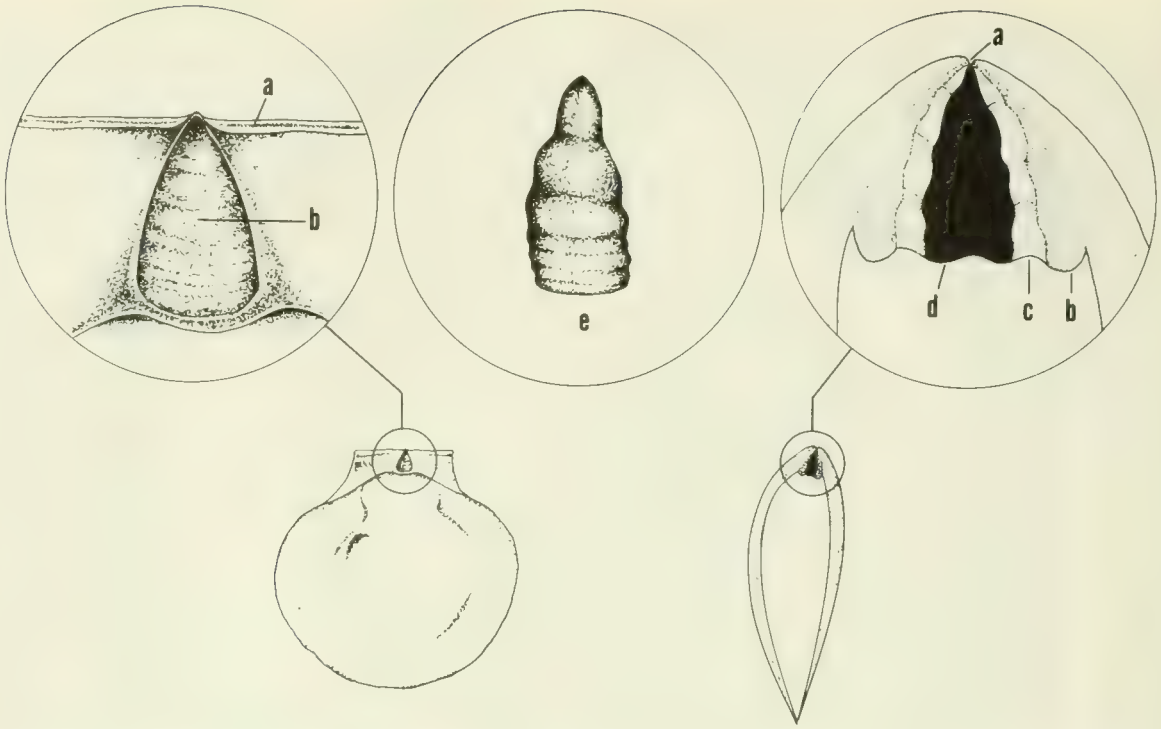

FIGURE 5.—Hinge and ligament of the sea scallop. (a) Outer layer of the ligament at hinge line, (b) resilifer, (c) calcareous plates of the resilium, (d) compressible part of the resilium, and (e) surface view of calcareous plate.

VALIDATION OF THE METHOD

In September of 1957, we had tagged and released 5,375 sea scallops on the northeast peak of Georges Bank. A fine hole is drilled in the ear of the upper valve just over the byssal notch in the lower valve. A stainless steel pin, bearing a numbered Petersen disc and a 6-inch yellow plastic streamer, is pushed through the hole and bent over to hold the tag securely (fig. 12). The animal is not wounded but the disturbance of dredging, handling, and tagging is sufficient to put a strong shock ring on the shell. The margin is nicked with a triangular file so that this tagging shock ring can be identified with certainty later. After recapture it is simple to measure how much new shell has been added since the date of tagging and, with a large enough sample, calculate the growth rate.

This particular tagging experiment had been very successful and we had a great many shells from recaptured animals. One group of 411 had been recaptured only a few weeks after release and therefore had added very little new shell. With the techniques described previously, the annual rings on this group were located and the shell lengths at the time of formation of each ring measured (table 1). The Walford (1946) regression equation calculated from the average length at the time of ring formation is: $L_{t+1}=42.4+0.706\ L_t$ (equation 1).

We also had 392 shells from animals that had been captured, tagged, and released at the same

TABLE 1.—*Average length (mm.) at time of ring formation for 8 year classes in sample of 411 sea scallops and average for all year classes combined*

Ring No.	Year class								Average
1	22.0	20.4	21.3	20.6	23.5	21.1	18.9	24.7	20.7
2	54.1	52.7	52.1	50.7	55.5	50.6	52.7	56.3	52.6
3	84.4	80.8	80.5	78.6	79.6	78.2	80.3	83.3	80.7
4		100.9	100.3	97.4	97.9	97.8	97.9	99.1	98.7
5			112.4	110.7	110.5	109.4	110.5	110.3	110.6
6				120.4	119.9	119.3	119.6	119.2	119.7
7					126.4	126.9	127.4	126.3	126.7
8						132.2	132.3	131.8	132.1
9							136.1	136.2	136.1
10								139.2	139.2
Number in year class	36	74	98	88	50	36	17	14	

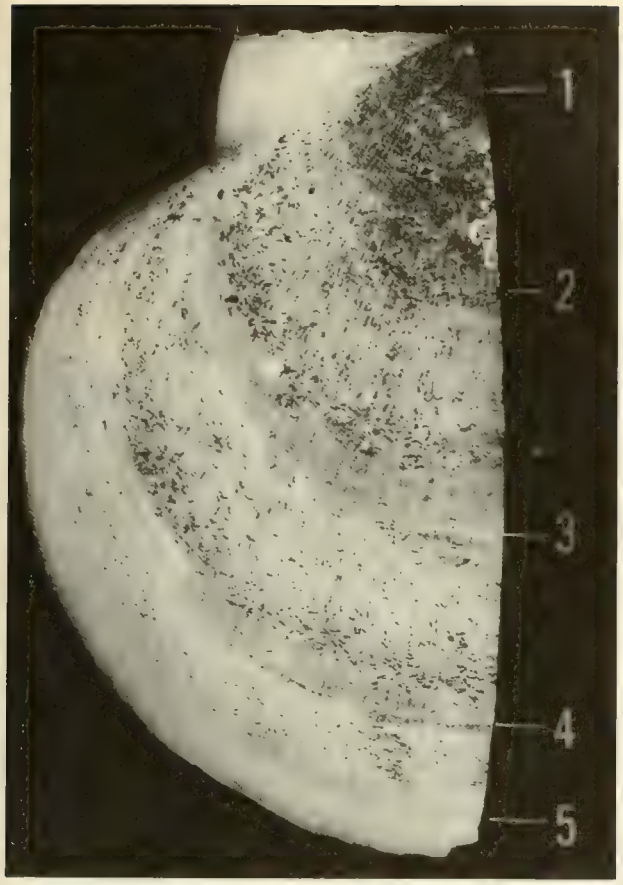

FIGURE 6.—Sea scallop shell with five prominent annual rings. The shell between the rings shows annual attacks by boring organisms.

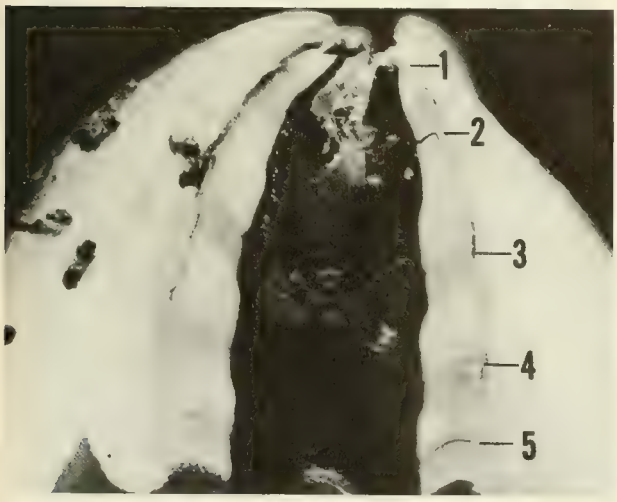

FIGURE 7.—Cross section of hinge of sea scallop showing annual marks in the calcareous plates of the resilium.

FIGURE 8.—Calcareous plate of a resilium showing banding and constriction in response to some annual stress.

time and location but which had been at large from 48 to 68 weeks before being recaptured. These shells were grouped by 2-week intervals, and the length when tagged (L_g) and the length when recaptured (L_r) measured on each one (table 2). The Walford (1946) regression of length at recapture on length when tagged was then calculated for each of the five groups. The tabulation below shows the number in each sample, the time at large, and the slope and intercept of the regression equations.

Sample No.	N	Weeks out	Slope	Intercept
1	140	49.6	0.6384	50.30
2	89	58.1	.6430	50.53
3	46	60.7	.6601	48.16
4	62	64.1	.5897	57.20
5	55	66.7	.5879	57.42

These regression equations, each of which represented growth for a different time interval, were then transformed to a common, 52-week, time interval using Lindner's (1953) method.

Sample No.	Weeks out	Slope	Intercept
1	52	0.6248	52.21
2	52	.6735	46.21
3	52	.7005	42.43
4	52	.6516	48.57
5	52	.6608	47.26

Taking an average slope and intercept gives $L_{t+1}=47.3+0.662\ L_t$ (equation 2) as the estimate of growth per year by this method.

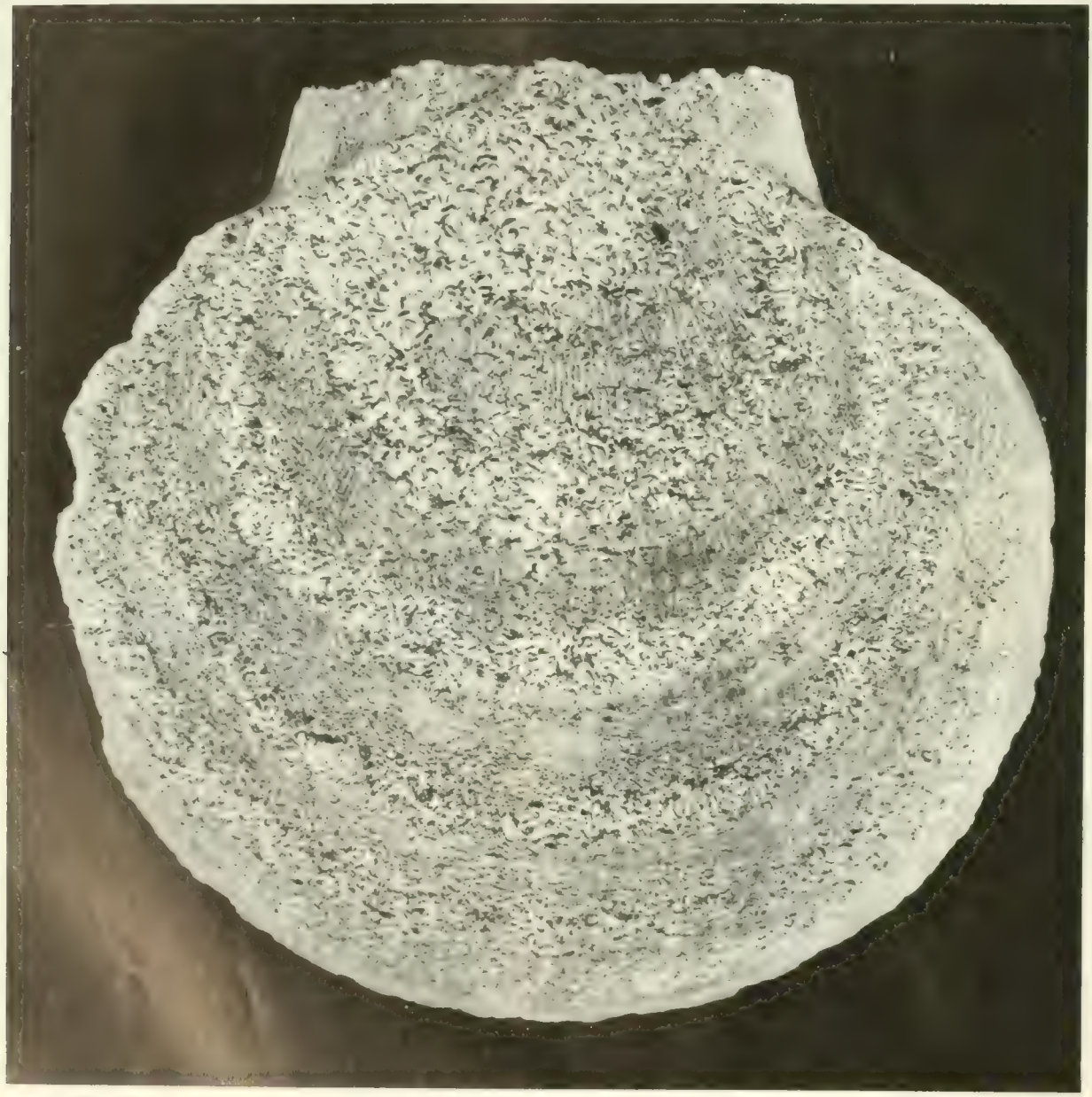

FIGURE 9.—Upper valve showing the result of heavy invasion of boring organisms. The annual rings are located between the areas of heaviest damage.

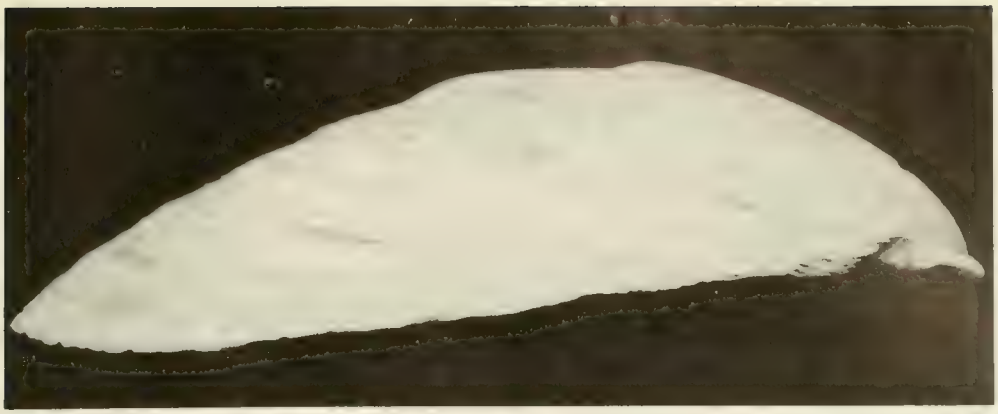

FIGURE 10.—Profile of the upper valve of a sea scallop. The annual rings are found in the areas of concave curvature.

TABLE 2.—*Length (mm.) of 392 sea scallops when tagged* (L_t) *and released at latitude 41°52′ N., longitude 66°23′ W., on Sept. 22, 1957, and when recaptured* (L_r) *about 1 year later*

SAMPLE 1, OUT 49.6 WEEKS

L_t	L_r	L_t	L_r	L_t	L_r	L_t	L_r	L_t	L_r
85.0	109.6	102.2	115.0	111.9	120.5	119.2	126.9	125.4	128.7
89.1	110.2	102.5	120.6	112.0	124.9	119.2	127.7	125.4	130.7
89.9	107.1	102.6	116.1	112.2	120.9	119.2	132.3	125.7	135.0
90.1	104.7	102.8	120.6	112.3	125.9	119.3	122.3	126.2	129.4
90.8	110.1	103.3	113.8	112.8	123.1	119.4	126.2	126.3	133.1
90.9	111.0	104.2	117.3	114.0	120.0	119.5	122.3	126.5	129.4
91.0	106.5	104.7	115.7	114.1	123.2	119.6	125.1	126.5	132.1
92.0	109.8	105.0	113.9	114.7	123.4	119.9	124.1	126.7	132.2
92.2	106.8	105.7	115.0	114.7	123.6	120.0	127.7	126.7	132.4
93.6	112.0	105.9	115.0	115.2	117.7	120.2	127.7	127.4	131.8
95.3	115.0	106.4	120.0	115.5	124.1	120.2	129.3	127.4	132.6
95.4	114.9	107.0	117.9	115.9	121.4	120.6	125.4	127.7	132.0
95.6	108.5	107.1	119.6	116.1	125.1	120.6	125.6	127.8	130.7
96.3	113.2	107.1	120.0	116.1	127.7	121.1	126.1	128.7	131.5
96.5	113.9	108.2	115.7	116.3	127.2	121.2	124.3	129.4	134.2
96.6	102.2	108.7	119.0	116.4	124.0	121.3	127.4	129.8	137.0
97.1	117.1	108.9	117.2	116.4	126.0	121.3	129.8	130.4	135.0
97.4	112.0	109.1	121.8	116.9	123.0	121.4	125.4	131.0	136.4
97.5	119.8	109.6	119.3	117.1	123.3	121.8	125.8	131.3	133.4
97.6	109.3	109.8	122.8	117.4	126.5	122.4	130.2	131.6	135.8
99.5	116.1	110.2	120.4	117.8	126.7	122.5	126.5	131.6	136.1
100.5	113.6	110.2	121.6	117.9	122.5	122.8	126.2	131.8	134.4
101.3	109.2	110.4	122.3	118.0	125.6	122.9	130.8	132.6	139.4
101.5	107.5	111.6	119.0	118.0	126.5	123.6	126.9	132.8	135.8
101.6	108.6	111.6	122.0	118.0	127.9	123.7	125.0	133.4	136.9
101.6	115.0	111.6	122.4	118.2	126.2	123.7	126.4	133.7	137.6
101.7	115.4	111.7	123.7	118.6	125.3	123.7	129.9	134.3	137.6
101.8	113.1	111.7	123.0	118.8	125.6	124.9	132.8	134.4	136.6

SAMPLE 2, OUT 58.1 WEEKS

L_t	L_r	L_t	L_r	L_t	L_r	L_t	L_r	L_t	L_r
85.6	106.0	100.7	120.0	111.8	120.4	119.2	125.0	127.1	134.7
86.9	107.3	101.7	115.8	112.4	120.5	119.7	129.1	127.2	133.5
87.9	105.1	101.8	111.6	112.6	126.2	120.0	129.3	128.5	136.4
88.8	113.9	103.0	116.6	113.3	120.4	120.6	129.9	129.7	133.4
90.3	115.3	103.5	115.2	113.5	119.4	121.0	126.0	130.7	137.6
90.9	103.0	104.5	115.2	113.9	123.8	121.3	126.0	130.9	135.0
90.9	108.3	104.9	115.6	114.4	120.6	121.4	128.5	131.0	134.5
90.9	114.4	105.0	117.2	115.0	125.6	121.9	127.0	131.0	135.3
91.8	105.7	106.2	117.4	115.4	123.9	122.8	134.1	132.9	135.4
91.9	112.3	106.3	118.5	115.6	125.4	122.9	127.9	133.7	136.7
94.7	107.5	107.1	121.8	115.9	127.1	124.0	133.8	133.8	138.3
95.0	115.3	107.2	118.9	115.9	127.5	124.6	129.7	133.9	136.4
95.3	113.3	109.1	116.9	116.1	124.0	124.9	128.1	134.0	137.3
98.6	110.4	109.4	118.7	116.2	125.6	125.0	128.9	134.4	140.6
98.6	116.1	110.7	118.5	117.4	123.3	126.0	133.4	134.6	136.1
99.4	114.8	110.8	124.0	117.8	123.5	127.0	131.5	136.1	136.7
99.6	116.2	111.1	121.2	118.2	124.7	127.0	133.8	141.1	143.1
100.5	118.9	111.7	126.0	118.7	121.9	127.1	130.9	------	------

TABLE 2.—*Length (mm.) of 392 sea scallops when tagged* (L_t) *and released at latitude 41°52′ N., longitude 66°23′ W., on Sept. 22, 1957, and when recaptured* (L_r) *about 1 year later*—Continued

SAMPLE 3, OUT 60.7 WEEKS

L_t	L_r	L_t	L_r	L_t	L_r	L_t	L_r	L_t	L_r
85.5	106.0	99.3	113.2	108.3	123.3	117.7	122.7	127.1	131.7
90.4	106.8	100.8	114.3	109.7	117.0	119.1	128.8	129.8	131.9
93.0	109.4	102.1	111.5	110.7	121.2	120.8	127.8	130.4	132.9
94.8	111.0	102.1	116.5	110.9	117.2	121.5	126.5	133.1	137.6
96.3	114.9	104.8	117.3	111.4	116.8	121.9	126.3	133.3	136.0
97.7	113.9	104.9	118.2	112.9	125.9	123.4	131.4	133.9	137.1
97.8	119.6	105.5	119.8	113.0	119.8	123.9	129.9	135.4	140.1
98.0	110.0	106.4	118.1	114.2	126.5	124.6	131.7	135.9	137.3
99.0	106.5	108.2	124.4	116.0	124.0	126.7	130.1	147.3	147.7
99.0	115.7	------	------	------	------	------	------	------	------

SAMPLE 4, OUT 64.1 WEEKS

L_t	L_r	L_t	L_r	L_t	L_r	L_t	L_r	L_t	L_r
86.2	110.3	99.3	120.8	109.2	123.3	116.4	123.3	125.4	131.4
87.6	107.3	99.7	118.3	109.3	115.5	116.4	125.1	127.5	131.6
88.9	110.9	99.7	118.5	109.9	119.6	117.9	125.7	128.9	130.8
90.2	110.0	100.5	113.1	110.9	120.3	118.4	125.2	129.1	136.5
93.1	117.3	101.2	117.0	111.5	122.9	119.2	125.2	129.2	134.6
93.5	115.6	101.3	118.1	111.5	123.5	120.5	131.4	129.7	134.4
93.9	113.3	104.1	121.0	111.6	124.0	121.3	133.6	130.3	132.5
95.9	114.0	104.3	119.5	111.9	123.0	122.0	128.5	133.3	140.2
97.4	114.0	105.1	120.7	113.3	122.4	122.5	132.4	136.6	138.3
97.6	114.3	105.7	121.5	113.9	122.8	122.9	128.2	137.9	139.0
97.6	121.8	106.0	118.5	115.5	119.3	123.4	129.2	138.4	140.1
98.2	113.2	107.6	112.9	115.7	124.1	123.8	129.2	143.7	145.5
98.5	108.1	108.4	117.4	------	------	------	------	------	------

SAMPLE 5, OUT 66.7 WEEKS

L_t	L_r	L_t	L_r	L_t	L_r	L_t	L_r	L_t	L_r
86.8	104.8	104.2	116.2	111.5	126.1	117.9	125.1	128.5	130.1
92.2	117.9	105.7	119.2	112.9	121.1	120.9	130.6	128.6	130.5
93.1	114.5	105.9	115.3	114.2	126.5	121.0	128.8	129.5	131.0
94.8	117.5	106.7	119.2	114.9	121.7	122.1	127.7	129.7	131.1
95.1	116.2	107.6	123.3	115.1	120.4	122.3	128.0	129.8	132.7
95.1	117.7	107.8	120.1	115.2	127.5	123.5	127.4	130.3	134.0
98.6	115.3	109.3	120.3	115.3	126.7	124.7	127.7	130.4	136.8
100.1	113.3	109.4	120.6	116.7	124.9	125.6	133.2	136.7	138.2
100.8	116.0	110.2	119.2	116.8	123.9	126.9	132.2	139.3	140.2
100.8	116.8	110.3	127.5	117.2	128.9	127.0	137.5	141.8	143.7
100.9	113.0	110.4	124.2	117.8	125.5	128.2	132.4	149.3	150.1

FIGURE 11.—Upper valve of a sea scallop showing seasonal change in color.

We have calculated the length at age for the 4 years following recruitment of sea scallops to the fishery using both growth-rate equations.

Item	Age				
	t	$t+1$	$t+2$	$t+3$	$t+4$
Equation 2	85.0	103.7	116.1	124.3	129.7
Equation 1	85.0	102.4	114.7	123.4	129.5

It is clear that the two equations, derived by different methods, give essentially the same results. We, therefore, have confidence in growth rates calculated by either method, and that our methods of locating annual rings are valid.

AGE AT RING FORMATION

It is interesting to note that, despite the strong check mark put on the shell at time of tagging, the tags apparently did not inhibit growth. Also, if we assume that there is little seasonal variation in the growth rate on Georges Bank, for those scallops that had been out for about a year, we can estimate the time of year when the annual ring is

laid down from the position of the ring on the shell between the check mark made at time of tagging and the margin. On this basis, the 1958 ring appears to have been laid down about 27 weeks after the date of tagging. This places ring formation at March 30, just 6 months after October 1, which is the usual date of spawning by sea scallops in this area (Posgay and Norman, 1958). The true age at the time of ring formation in this area is, therefore, the number of the ring minus one-half year. There is a possibility, now under investigation, that the first definable ring, at about 20 mm., is not laid down during the first year of life but rather in the second.

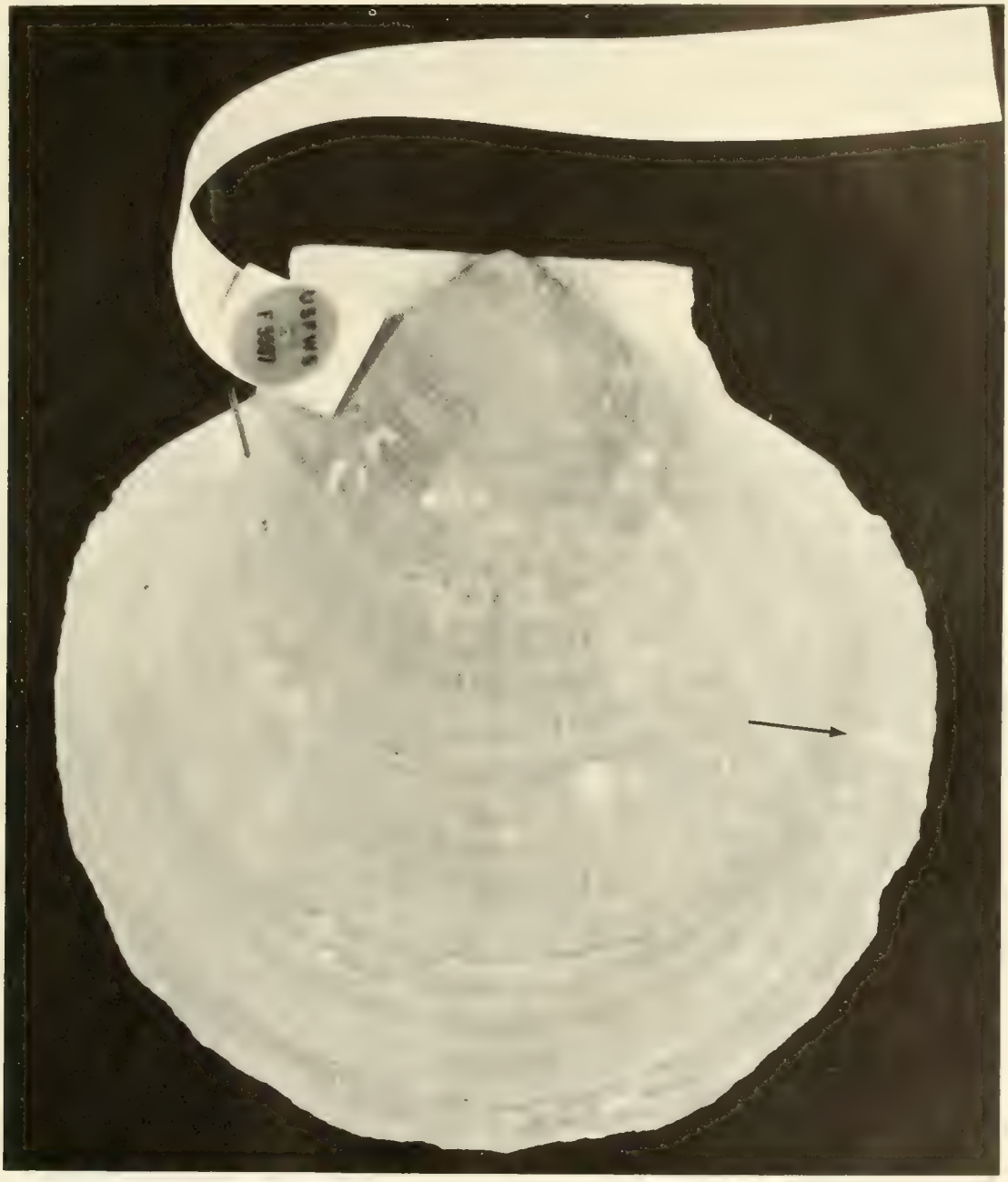

FIGURE 12.—Upper valve of a sea scallop that has been tagged, released, and recaptured. (The arrow points to the nick which was made in the margin at the time of release.)

TABLE 3.—*Age structure and average length (mm.) at time of ring formation in sample of 351 sea scallop shells determined independently by 2 readers*

Number of rings on the shells	Average length							Grand average
	3	4	5	6	7	8	9	
Reader No. 1:								
Ring number								
1	21.6	20.4	19.6	19.8	19.6	18.0	17.9	19.6
2	58.3	54.6	53.9	55.4	55.2	53.2	54.7	55.0
3	84.5	80.8	79.9	83.4	81.0	81.3	80.1	81.6
4		95.9	96.0	99.3	98.3	100.9	95.9	97.7
5			106.9	109.9	110.3	113.3	109.2	109.9
6				116.8	117.6	122.4	117.9	118.7
7					123.0	128.1	125.4	125.5
8						131.2	131.5	131.3
9							133.8	133.8
Number in ring group	85	71	75	57	37	17	9	
Reader No. 2:								
Ring number								
1	21.2	20.5	20.0	19.7	19.7	19.9	18.2	19.9
2	56.1	53.2	53.8	55.0	54.9	51.5	54.9	54.2
3	85.8	83.5	81.2	82.5	81.2	79.7	80.8	82.1
4		98.7	98.3	99.8	98.6	98.7	97.7	98.6
5			109.2	111.9	110.6	110.5	109.1	110.3
6				118.6	118.4	120.4	118.4	118.9
7					123.8	126.7	125.6	125.4
8						130.1	131.5	130.8
9							133.5	133.5
Number in ring group	93	87	66	47	34	12	12	

OBJECTIVITY OF THE CRITERIA

To test whether our criteria for determining which annuli were annual rings were sufficiently objective, a summer assistant, William Evoy of Reed College, was trained in the reading technique. He was then given a sample of 351 shells to age and measure, after which the same sample was read by the senior author.

The correspondence of results was very good (table 3). There was disagreement on the number of rings, but never by more than one, on about 10 percent of the shells and a few additional disagreements as to position of the annual ring. The growth-rate equations calculated from the two sets of data were virtually indistinguishable, as shown in the following formulae:

$$L_{t+1}=37.49+0.7384L_t$$

$$L_{t+1}=36.75+0.7467L_t$$

SUMMARY

The shell of the sea scallop, in common with many other mollusks, bears annual rings but they are frequently weak and ill-defined or masked by the presence of other annuli caused by nonannual phenomena. By using annual marks on the resilium, changes in shell curvature, changes in color pattern, weight of the shell, and areas of attack by boring organisms it is usually possible to localize the position of the annual rings so that they can be found by intensive examination.

These methods have been validated by showing that a growth rate calculated from the annual rings was almost identical with a growth rate calculated from the growth of tagged and recaptured animals from the same area.

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DYNAMICS OF A PENAEID SHRIMP POPULATION AND MANAGEMENT IMPLICATIONS

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ABSTRACT

In assessing present utilization of a stock of pink shrimp (Penaeidae) that supports an important commercial fishery in the eastern Gulf of Mexico, the interaction of population growth and mortality is critically analyzed. Estimates of the parameters involved were secured through a mark-recapture experiment wherein a biological stain served as the marking agent. The experiment was oriented in space and time so that exploitation of the marked population, which initially consisted of individuals uniform in size, provided measures of growth and mortality in the parent age group during and immediately following its transition from prerecruit to postrecruit status. Throughout the experiment, the entire stock as well as the marked population were heavily fished. Upon examining the question of whether or not the fishery's production could be improved by postponing the start of fishing until the shrimp reach a size greater than the 70 headless-count designation now generally viewed as a practicable minimum, it was noted that expected growth, although relatively high, would be insufficient to offset substantial losses due to expected natural mortality. Even with a moderate increase in growth rate, an appreciably reduced natural mortality would have to be indicated before such a move could be considered feasible. Maximum potential yield in both weight and value is obtained with the minimum acceptable size that the fishery currently imposes.

Broadly speaking, the basic goal of biological research undertaken by the Bureau of Commercial Fisheries is to gain the best possible understanding of how fishing and the principal environmental factors (once they are determined) govern the size of commercial fishery resources, and hence the yield of fish and fishery products. Its attainment would, theoretically, enable us to establish guidelines for maintaining any resource at about that level where production or, perhaps, economic advantage is highest. One should not gain the impression, however, that such a level can be held static over long periods of time, but recognize instead that it is subject to fluctuation from year to year in response to an everchanging environment and thereby presupposes continual readjustment of fishing intensity.

Utilization is associated very closely with the concept of resource maintenance. In the con notation of the phrase "conservation of natura resources," maintenance and utilization are, in fact, not mutually exclusive. But it is always likely that long before research can produce a scheme for effective resource maintenance, it will provide ad interim some indication of how a resource should be best utilized. Fishery research, which largely embraces the field of population ecology (including dynamics), becomes most efficient when it programs for short-term or intermediate as well as long-term objectives. It is noteworthy that the processes of achieving both types of objectives very often require the same basic data.

For nearly as long as Gulf of Mexico shrimp resources have been exploited, concern has prevailed as to whether they have always been utilized to best advantage. Many believe that the minimum size of commercially acceptable

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shrimp should be increased, that the harvesting of any age group (or "brood") should be delayed until, by virtue of a high growth potential, maximum (or at least a greater) weight or biomass is reached. Phrased more simply, the question posed and heretofore not answered satisfactorily is: At what size per individual should an age group of shrimp begin to be harvested so as to realize the maximum yield from that group during its life span?

This question has important economic implications and requires that we understand the relationships between, and can measure, the rates of two concurrent biological processes: (1) *Growth*, the increase in shrimp size per individual per unit time, and (2) *mortality*, the numbers of shrimp dying per unit time (particularly due to natural causes).

Over the years, fishery biologists have found population growth and mortality parameters highly elusive. Recently, however, as part of its long-range shrimp research program, the Bureau of Commercial Fisheries perfected a very satisfactory process of marking shrimp that now permits such parameters to be approximated by the useful mark-recapture technique. The marking system proving so successful is the stain-injection method. Menzel (1955) is generally credited as having conceived its use on shrimp; Dawson (1957) as having substantiated its potential by means of laboratory experimentation; and Costello (1959, 1964) and Costello and Allen (1960) as having developed its large-scale application afield.

This paper first presents the results of a mark-recapture experiment with a rather well-defined stock of pink shrimp, *Penaeus duorarum* Burkenroad, which supports an important commercial fishery in southwest Florida, the widely known Tortugas fishery. After documenting the required estimates of growth and mortality, the paper then describes their synthesis through a theoretical yield equation to attempt an answer to the question stated earlier. In so doing, it draws in small part on the results of yet another mark-recapture experiment conducted with the same species, but for a different purpose, just prior to the one of primary interest.

Though it was classified as merely preliminary and expanded efforts were to be scheduled only if it achieved any reasonable degree of success, the Tortugas experiment proved successful well beyond our somewhat modest expectations. The quality of the resulting data is reflected in the kind of treatment they are given here. Such extensive treatment, regardless of the experiment's outcome, had not been anticipated in advance.

TORTUGAS MARK-RECAPTURE EXPERIMENT

DESCRIPTION AND REGULATION OF FISHERY

Lying west of Key West, Fla., reaching little beyond the 30-fathom contour, and extending not much farther northward than the 25th parallel, the Tortugas trawling grounds seasonally experience some of the most intense shrimp fishing seen in the Gulf of Mexico (fig. 1). Stimulating this activity is the appearance of large numbers of subadult pink shrimp which emerge in closely spaced surges from the shallow "nursery" grounds in Florida Bay to the east.[1] Although maturing shrimp may enter the fishing grounds at all seasons, it is in September-March that migrations are greatest and fishing is heaviest. Practically all fishing occurs at night when the pink shrimp is most active and hence most vulnerable. Like its close relative the brown shrimp, *P. aztecus* Ives, this species usually burrows and is therefore comparatively inaccessible during the hours of daylight.

Most trawlers operating on the Tortugas and adjacent grounds are of the characteristic Florida design (fig. 2). For all practical purposes they are nearly uniform in size and power, and employ fishing gear of roughly the same specifications (Iversen and Idyll, 1959; Kutkuhn, 1962).

The Tortugas fishery together with a lesser one, the Sanibel fishery, which is centered roughly 100 nautical miles to the north, did not become well established until the early 1950's (Idyll, 1957). A question often raised and now being examined is whether populations supporting both fisheries are genetically discrete, or whether they are continuous—even though continuity may prevail only at widely spaced life history stages. Evidence acquired to date tends to support the assumption made in this study that the Tortugas fishery largely depends on a stock of pink shrimp which is essentially separate from that sustaining the Sanibel fishery (Costello and Allen, 1960; 1961).

[1] Idyll (1957), Dobkin (1961), and Cummings (1961) should be consulted for a detailed account of pink shrimp life history.

FIGURE 1.—General area in which mark-recapture experiments were conducted. Large numerals (1–4) identify coastal subareas employed in tabulating fishery statistics. Data shown in subarea 2 refer to the Tortugas experiment (September–December 1961), those in subarea 4 to the Sanibel experiment (December 1960–June 1961).

Annually contributing about 10 percent to the total Gulf production of shrimp, landings in the Tortugas fishery reached a peak of 23.6 million pounds in 1960, having risen from almost a record low of 12.9 million pounds the year before. The latter value represented a 44-percent drop from the previous high of 23.0 million pounds landed in 1958.[2] Since 1956 the fishery has seemingly had

[2] Source: Gulf coast shrimp data, published monthly by the Branch of Fishery Statistics, Bureau of Commercial Fisheries, U.S. Fish and Wildlife Service.

FIGURE 2.—Double-rigged, Florida-type trawlers predominate in the Gulf of Mexico shrimp fleet.

to rely to an increasing extent on small shrimp to keep production at a profitable level (Kutkuhn, 1962).

Believing that utilization might be improved by inhibiting the harvest of small shrimp, the Florida State Board of Conservation established in 1957 what is called a "control" area (Ingle, Eldred, Jones, and Hutton, 1959, figs. 1–3). This area was so situated that the preponderance of shrimp entering the open fishing grounds ostensibly migrated through it. Fishing was not to be permitted in the control area whenever periodic surveys disclosed that the shrimp therein were smaller than the size at which 50 headless and uniformly sized individuals weigh 1 pound. This regulatory concept was revised in mid-1961 when the Board delineated a permanently closed conservation area which incorporated part of the earlier control area and extended the latter's boundaries to enclose all of Florida Bay (fig. 1). Also circumscribed was a less extensive management (control) area from which only shrimp of 60 "headless-count" or larger may be taken.

MARKING PHASE

The Tortugas mark-recapture experiment was designed to take complete advantage of the physical and regulatory features of the fishery. Shrimp destined to make up the experimental population were to be captured, marked, and released just prior to the onset of heaviest expected fishing intensity. Concentrations of precommercial-size shrimp moving through the State management area offered the opportunity to

establish an experimental population from which could be obtained measures of growth and mortality in the parent population before and during as well as after its transition from prerecruit to postrecruit status.

Accordingly, operations using facilities provided by the Bureau's M/V *George M. Bowers* got underway on September 18, 1961, with the first releases of marked shrimp being made 2 days later. Shrimp were captured with small-mesh trawls hauled for very short intervals of time (frequently not more than 2 minutes) to minimize injury caused by compression in the net. To insure that only shrimp in prime condition entered the experiment, catches were held in tanks of circulating sea water for periods of at least 12 hours. After all weak and dying individuals had been removed, the remainder was sorted so that only those falling into a specified size range (total length) were retained for marking. This range was arbitrarily set using as a point of reference the modal length of available shrimp, such length having been determined by sampling catches made at the start of operations. Graded individuals were then marked by carefully injecting small quantities of a 0.25-percent aqueous solution of Trypan blue stain. Groups of marked shrimp were observed for at least 4 hours before being released, only the most vigorous individuals at the end of that time being selected for the experiment. These were released in lots of 100 at scattered sites and at irregularly spaced intervals during the marking period by means of a special release box (Costello, 1964). This device permitted the experimental shrimp to be returned directly to the bottom from whence they came (the depth being about 12 fathoms), and precluded large-scale losses due to predation by fishes and birds that would have occurred had the shrimp been released at the surface. Underwater movies taken during this operation reveal that marked shrimp released from the box immediately burrowed into the bottom, thereby satisfying the assumption that predation losses were, for all practical purposes, nonexistent. Because of judicious handling, selection, and release of the experimental material, it is hereinafter assumed that the total number of marked shrimp reintroduced into the parent population represented the actual or "effective" size of the marked population established during the marking period.

In the manner just described, an experimental population of 2,090 individuals was created within a 4-day period. Figure 1 shows the general location of capture and release sites. Measurements from an accumulation of small samples drawn each time a group of shrimp was released provided essential information concerning the population's length and weight attributes at the start of the experiment (table 1).

COMMERCIAL FISHING OPERATIONS DURING EXPERIMENT

Greatly influencing the outcome as well as the utility of results of experiments like the present one are the amount and distribution of recapture effort relative to the distribution of the experimental population. With all other potential sources of bias inoperative or satisfactorily accounted for, the rate at which marked individuals are recaptured becomes simply a function of the probability of recapture.[3] An index of this probability is, logically, the intensity of fishing or, in a rather restricted area such as is involved here, the fishing effort. A major problem is that the fishing effort often does not remain constant and thereby confounds the probability of recapture. It must be assumed at the outset, of course, that the experimental population soon reintermingles with and behaves in the same manner as the parent population (age group) from which it was temporarily removed.

Detailed information of fishing operations during the Tortugas experiment was provided by the Bureau of Commercial Fisheries Branch of Fishery Statistics which has agents stationed at major Gulf ports, including Key West, Fort

TABLE 1.—*Sex, length, and weight data from samples of the marked population at the beginning of the Tortugas experiment, middle of week ending Sept. 23, 1962*

[Number in marked population: 2,090. Estimated sex ratio: 60♂:40♀]

Sex	Number sampled	Carapace length[1]		Total length		Total weight	
		Mean	Range	Mean	Range	Mean	Range
		Mm.	*Mm.*	*Mm.*	*Mm.*	*G.*	*G.*
Male	168	19.2	17.9–20.1	90.1	84.2–94.1	5.9	4.8–6.8
Female	110	19.5	18.5–20.2	88.9	84.2–94.1	6.0	5.2–6.7
Total	278	19.3	17.9–20.2	89.6	84.2–94.1	5.9	4.8–6.8

[1] Carapace length is defined as the straight-line distance from the posteromost edge of the orbit to the posterior edge of the carapace where it intersects the middorsal line.

[3] Throughout this report, "recapture" refers to the marked shrimps' capture by the fishing gear; in contrast, "recovery" refers to their subsequent detection in commercial catches (or landings).

Myers, and Tampa, Fla. Estimates of the total effort expended weekly on the Tortugas grounds had to be projected from sample interviews (n) with trawler captains landing their catches at these ports. The procedure simply consisted of estimating from the sample data the average number of hours fished during each fishing trip and multiplying this by the total number of trips as determined by a canvass of processing plant records. Thus, the total hours fished in any week is given by

$$\hat{X}=N\bar{x}=\frac{N}{n}\sum_{1}^{n}x_i \qquad i=1, 2, 3, \ldots n$$

where N is the total number of trips by individual trawlers to the fishing grounds, x_i is the number of trip-hours fished as reported by the captain of the i^{th} vessel entering a weekly sample, and $\bar{x}=\frac{\sum_{1}^{n}x_i}{n}$ is the sample estimate of the mean number of hours actually spent fishing during each trip. The only difficulty arose when "uninterviewed" trips ($N-n$) extended over periods of more than 1 calendar week. In such cases, fractional trips for each of any 2 adjoining weeks had to be designated. These fractions were then summed together with trips contained entirely within respective weeks to obtain the weekly totals. Variances of the sample estimates were also calculated and, under the assumption of negligible or constant sampling bias, provided the estimates of total effort with an index of reliability. Hence

$$v(\bar{x})=\frac{\sum_{1}^{n}(x_i-\bar{x})^2}{n(n-1)}\cdot\left(\frac{(N-n)}{N}\right)$$

and

$$\text{confidence interval } (\hat{X}):\ \hat{X}\pm tN\sqrt{v(\bar{x})}$$

where t is the value of the normal deviate corresponding to the desired confidence probability.

The Tortugas experiment lasted about 14 weeks; table 2 gives effort statistics and estimates, together with total landings, for each week plus the two that immediately preceded the start of the experiment. To provide some indication of how the effort was distributed on the fishing grounds, the weekly totals are also apportioned (on the basis of interview data) among three well-defined depth zones. Landing figures are not estimates but accumulations of actual catch weights obtained through a continuing canvass of all processing plants.

One other matter that will warrant consideration in a later section relates to the stage in age group development at which the member shrimps' commercial acceptance becomes complete, or selectivity no longer constitutes a factor. As employed here, the word "selectivity" does not refer to the selective properties of fishing gear but means, rather, the purposeful avoidance of shrimp of undesirable size even though they may be largely vulnerable to the gear in general use. Such selection is ordinarily accomplished by sorting catches or by test fishing for aggregations in which most individuals are of marketable size.

Unfortunately, the minimum marketable size of shrimp varies within the industry (or according to State law) from area to area around the Gulf, and in some localities may be only vaguely defined (or not stringently enforced). During the Tortugas experiment the fishery did not recognize a specific minimum size, with the result that sorting catches for the purpose of discarding small shrimp was not practiced. In fact, the only form of selection evident was the weekly expenditure of comparatively small amounts of fishing effort prior to the period in which the greater proportion of available shrimp reached a size of about 70 headless-count.

Examination of size (weight) frequency curves obtained from landings during the study period disclosed that selective fishing solely for medium and large shrimp was, practically speaking, inoperative (fig. 3). It suggested further that shrimp somewhat below the size designated herein as the minimum acceptable size (70 headless-count) were, if not entirely, almost wholly vulnerable and actively sought out by a sizeable though undetermined portion of the fishing fleet. Figure 3 clearly shows that small (in many instances, very small) shrimp predominated in Tortugas catches during the last 15 weeks of 1961. This fact lends credibility to the assumption that bias due to the selective action of the fishing gear was negligible and that the retrieval of marked shrimp of a size well below that tacitly set as a commercial minimum was almost entirely governed by the probability of a piece of gear encountering and capturing them, even though such probability

TABLE 2.—*Commercial shrimping operations in Gulf of Mexico statistical subareas 1–3 (Dry Tortugas-Marquesas) during September–December 1961*

Item	Week ending							
	9–9	9–16	9–23[1]	9–30	10–7	10–14	10–21	10–28
Total number of trips (N)	41	77	81	88	80	88	35	115
Number of trips sampled (n)	7	15	21	19	23	27	16	26
Mean number of hours fished per trip ($\bar{x}$)	28.8	35.8	26.0	31.8	49.7	32.1	26.2	32.9
Variance of mean $v(\bar{x})$	22.0	10.8	5.8	20.1	8.1	6.9	5.8	3.1
Coefficient of variation	0.16	0.09	0.09	0.14	0.06	0.08	0.09	0.05
Estimated total effort in hours ($\hat{X}$)[2]	1,180±250	2,760±330	2,110±250	2,800±510	3,980±290	2,820±300	920±110	3,780±270
—at: 0–10 fathoms								
11–20 fathoms	1,180	2,760	2,110	2,600	3,720	2,770	920	3,780
21–30 fathoms				200	260	50		
Percent of total effort in Subarea 3	1	1	1	9	5	7	3	10
Total landings[3]	42.1	287.9	301.6	212.2	227.3	179.9	72.8	411.8

Item	Week ending								
	11–4	11–11	11–18	11–25	12–2	12–9	12–16	12–23	12–30
Total number of trips (N)	97	206	270	177	175	201	217	161	67
Number of trips sampled (n)	20	62	97	69	37	53	74	48	2
Mean number of hours fished per trip ($\bar{x}$)	41.7	28.3	37.3	30.7	39.9	44.4	42.1	35.9	24.0
Variance of mean $v(\bar{x})$	12.1	3.2	3.2	3.7	10.0	6.3	3.0	3.3	23.3
Coefficient of variation	0.08	0.06	0.05	0.06	0.08	0.06	0.04	0.05	0.20
Estimated total effort in hours ($\hat{X}$)[2]	4,040±440	5,830±480	10,070±630	5,430±440	6,980±730	8,920±650	9,140±480	5,780±380	1,610±420
—at: 0–10 fathoms						180	330	80	390
11–20 fathoms	3,680	5,600	8,760	4,890	6,840	8,060	7,820	5,380	1,190
21–30 fathoms	360	230	1,310	540	140	680	990	320	
Percent of total effort in Subarea 3	5	3	6	9	1	6	4	8	1
Total landings[3]	365.3	680.2	763.7	215.8	240.1	467.3	433.1	189.9	39.0

[1] Week in which experiment began.
[2] 0.80 confidence intervals.
[3] Thousands of pounds (whole shrimp).

was represented in part by purposively selective effort. It follows that the likelihood of recaptures being subsequently recovered from commercial landings had to be presumed essentially constant throughout the experiment regardless of shrimp size.

RECOVERY PHASE

Extensive publicity coverage preceded and continued during the experiment. With the assistance of the Bureau's Branches of Fishery Statistics and Market News, cooperation in the retrieval of stained shrimp was solicited through correspondence, market reports, and personal interview from all industry segments as well as from State conservation agencies and the Gulf States Marine Fisheries Commission. The press, radio, and television provided additional coverage. A reward of $2 was offered for the return of any marked shrimp when accompanied by information regarding its place and date of capture. Posters to this effect (fig. 4) were conspicuously placed in all processing plants adjacent to the area in which the experiment took place. Close contact with fishermen and processors was maintained at all times.

Return of marked shrimp began immediately with 47 having been recovered before the end of the experiment's first week, referred to herein as the "period of release." Fortuitously, the State management area in which the marked shrimp were released (fig. 1) was opened to commercial fishing 2 days after the experiment got underway. In all, 443 or 21 percent of the total number liberated were eventually recaptured and returned for verification.[4] Daily distribution of recaptures is shown in figure 5. To facilitate subsequent analysis, they are grouped by calendar weeks (top of fig. 5).

Recovery continued strong for the first 8 weeks, reaching a peak during the sixth week and then dropping sharply (fig. 5). No marked shrimp were recovered after the 13th week. This abrupt attenuation reflected a real decline in the experimental population since associated recapture (fishing) effort did not decrease but rose significantly. Emigration of marked shrimp from the range of effective fishing effort appeared negligible (fig. 1), with no individuals being taken beyond 20 fathoms (only two outside 15 fathoms) or north of the 25th parallel despite measurable expenditures of effort at both locations (table 2). In general,

[4] One marked shrimp returned 3 months after recapture was not included in subsequent analyses.

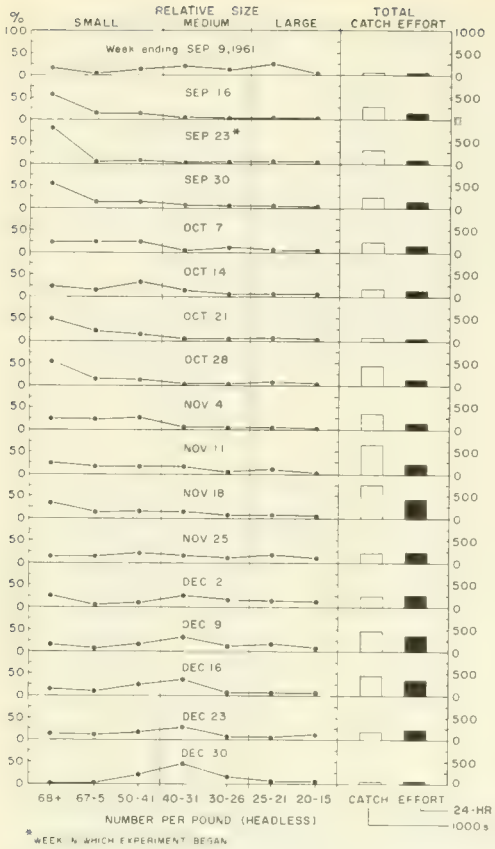
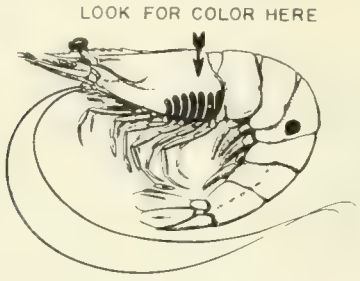


FIGURE 3.—Weekly commercial catch and effort statistics from the Tortugas pink shrimp fishery (statistical Subareas 1–3), September–December 1961.

what little movement was observed for the marked shrimp during the course of the experiment seemed to be in a west-northwesterly direction. As will be shown later, the week in which most marked shrimp were recaptured (sixth week, October 22–28) coincided with that during which the preponderance of the experimental population attained the "minimum" commercial size designated earlier. In other words, selective fishing by a heretofore undetermined portion of the fishing fleet ceased to be a factor at approximately this point.

Slightly less than three-fourths of the marked returns were detected while handling catches at sea. Because of the consistently small size of shrimp taken during the experiment (fig. 3), the great majority of catches had to undergo complete processing ashore. Such treatment entailed removing the head of each shrimp by hand, an

Shrimp have been marked with blue and green biological stains to obtain information on movements, growth, and rate of harvest. The color appears only on both sides of the head (in the gills) as shown in the illustration.



A reward of $2.00 will be paid for stained shrimp when returned with the following information:

1. Exact place the shrimp was caught.

2. Date the shrimp was caught.

Notify by mail the U.S. Fish and Wildlife Service, No. 1 Rickenbacker Causeway, Miami, Florida, or contact any Fish and Wildlife Service agent at port of landing. Please include name of vessel with the information submitted.

FIGURE 4.—Typical poster advertising reward for the return of marked shrimp. Blue stain was employed in both the Tortugas and Sanibel experiments.

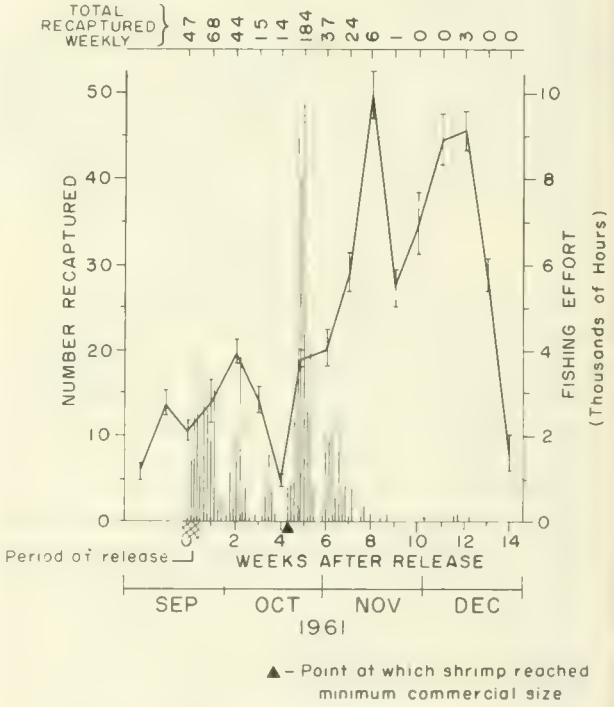


FIGURE 5.—Temporal distribution of fishing effort and of marked shrimp recaptured during the Tortugas experiment. Vertical bars from the abscissa represent number recaptured on indicated days. Vertical lines through points on effort curve define 0.80 confidence intervals for weekly effort estimates.

operation usually undertaken aboard the fishing vessel when most of the catch consists of medium-size or larger shrimp. Regardless of where beheading takes place, however, the chances of detecting marked specimens in the process are always very good to excellent. Under the conditions prevailing in most processing plants they are highest. All recovered shrimp not found at sea by vessel crews were later retrieved by plant personnel.

So far as is known, only a small fraction of all landings made within the study period escaped such close scrutiny, this occurring when landings infrequently had to be shipped directly to canneries located on the northern Gulf coast.

SANIBEL MARK-RECAPTURE EXPERIMENT

Though specifically designed for another purpose, the Sanibel experiment yielded growth data that proved useful in corroborating comparable data derived from the Tortugas experiment. By way of providing a brief description, the former experiment began about 9 months before the latter and extended over the period December 1960 to June 1961. In an attempt to determine the migration patterns of juvenile pink shrimp as they leave estuaries in the vicinity of Sanibel Island, Fla., 32,900 shrimp were marked with Trypan blue stain and released in Pine Island Sound. Commercial fishermen subsequently recaptured 155 (or 0.5 percent) at the locations indicated in figure 1.

Individuals making up the experimental population were first graded to uniform size though not nearly so carefully as those selected for the Tortugas experiment. A sample of 463 specimens taken at the experiment's start revealed a mean total length and corresponding weight of 75.3 mm. and 3.5 g., respectively. Sexes occurred in the estimated ratio of 46 males to 54 females.

ESTIMATION OF GROWTH

METRIC CONVERSIONS

Solution of the yield equation employed in a later section postulates that the average growth of each individual making up the population of interest be expressible in terms of weight, and that the average relationship between an individual's weight and length be firmly established.

Since it is ordinarily impractical to measure precisely in the ffeld the weight of animals as small as shrimp, sampled individuals for the most part must be measured as to length at the sampling site, or preserved (rarely frozen) and later measured, again according to some length criterion, at a more convenient time and place. Subsequently required in either case are appropriate means for converting length to weight units.

Three situations that are met in the course of studies like the present one, and in shrimp research generally, may thus be defined. The first entails reciprocal conversion of the linear size indices commonly used in shrimp work, viz, total and carapace length. In this study, for example, total length was the criterion used to grade shrimp selected for the Tortugas experiment. But the sample from which the actual size-range limits were determined had to be preserved (formalin) for later measurement under more favorable conditions. Since the total length of shrimp so treated cannot be accurately measured because of the distorting and hardening effects of the preservative, carapace length, which remains unimpaired, provides the most practicable index of shrimp size. The statistical relationship between total length and carapace length serves to transform either linear dimension to the other and proves particularly useful when comparing the results of research in which the methods of measurement differ from one study to the next.

The two remaining situations prevail where interest centers on the transformation of linear to weight units, i.e., (1) from total length to total weight when length measurements can be made at the time of sampling and (2) from carapace length to total weight when the sample material must first be preserved.

Over the period August 1960 to January 1961, and independent of the experiments reported herein, weight and corresponding length measurements were obtained from slightly more than 1,600 pink shrimp sampled from commercial catches taken along the east and southwest Florida coast (Biscayne Bay and the Tortugas-Marquesas area, respectively). An indication of their statistical strength in terms of sample distribution by sex and relative size is given in table 3.

TOTAL LENGTH-CARAPACE LENGTH RELATIONSHIP

A plot of the mean carapace lengths for each of 28 male and 36 female, 5-mm. total-length classes suggested that the relationship between the two attributes could be best described by a simple exponential (fig. 6). Up to a total length of about 150 mm. the relationship for both sexes appears nearly identical and is, for all practical purposes, rectilinear. Beyond this length, however, definite curvature indicates that increases in carapace length (c) do not keep pace with increases in total length (l). Note also in the larger shrimp a marked sex differential in the total length-carapace length ratio. Thus, for shrimp of the same total length, females will have a greater carapace length than males, the difference increasing with size.

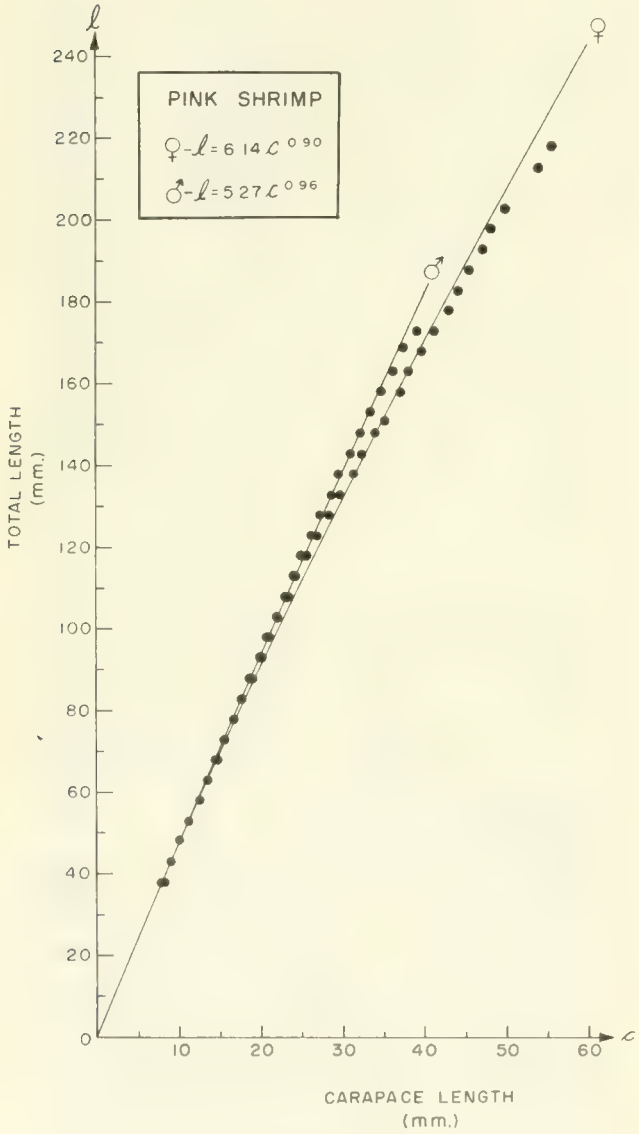


FIGURE 6.—Total length-carapace length relationship in pink shrimp.

TABLE 3.—*Distribution by sex and relative size of pink shrimp sampled during 1960–61 in south Florida for weight and length measurements*

Sex	Number of specimens measured	Range in total length	Number of 5-mm. length classes	Average number of specimens per class	Number of classes with less than 15 specimens
		Mm.			
Male	729	35–175	28	25	3
Female	888	35–215	36	26	3
Total	1,617	35–215	36	45	3

For pink shrimp not exceeding 170 mm. total length (equivalent to 16 headless-count), the information provided in figure 6 will permit, graphically or mathematically, reasonably accurate estimation of total length from a known carapace length. Although precision diminishes somewhat above this limit, resulting estimates will still be sufficient for most purposes.

Linear conversions indicated in table 1 and elsewhere in this study employed the information given in figure 6.

Weight-Length Relationships

Plots of data categorized as above showed weight to be a simple power function of length. Either the fitted curves or equations for total weight (w) as a function of carapace length (fig. 7), and as a function of total length (fig. 8) may be used to estimate weight from either linear dimension with reasonable precision and accuracy. Close examination revealed some seasonal variation in the relationships, but not enough to be of practical significance. Sex differences are clearly evident in each case with the disparity being particularly prominent in the total weight-carapace length ratios. Among shrimp having the same carapace length, males, on the average, not only possess a greater total length but are heavier than females. It follows, conversely, that in individuals of the same total length, the males will weigh less than the females and have a shorter carapace. These differences should be borne in mind whenever metric conver-

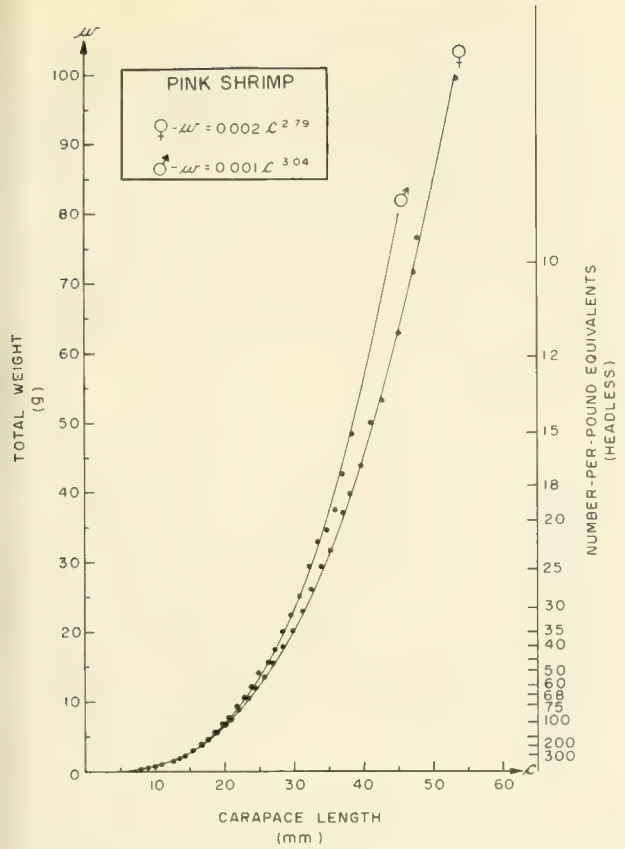


FIGURE 7.—Total weight-carapace length relationship in pink shrimp.

sions of the types treated here become necessary.

All length-to-weight conversions required in subsequent analyses are made with the information shown in figures 7 and 8.

Of particular interest in the present study is whether or not shrimp growth is isometric or, more specifically, whether or not the total weight-total length relationships derived above conform to the well-known cube law, viz, $w=al^b$, where $b=3$. Conformation (or lack thereof) should be acknowledged when growth and mortality parameters are integrated to solve the yield equation referred to earlier and described in a later section. The fact that the parameters of the mathematical expressions relating total weight to total length proved almost identical for both sexes (fig. 8) simplified somewhat their statistical assessment. Upon being tested with sexes separate or combined, the hypothesis of no exponents differing significantly from $b=3$ had to be rejected. [For sexes combined—H_0: $b=3.00$ when in fact $b=3.14-t=11.16$, compared with $t_{.05}$ (33 degrees of freedom) $=2.04$.]

ESTIMATING GROWTH PARAMETERS AND FITTING CURVES

Recaptures from the Tortugas experimental population provided some of the best data yet obtained for describing growth in North American Penaeidae (table 4). In synthesizing these data for practical application later, a growth differential between sexes materialized as the only real impediment, there being no evidence of growth inhibition by the mark employed. Ideally, growth constants for both sexes should be treated separately (via summation methods) in all yield predictions, particularly since the maximum size attained by male shrimp appears to fall far short of that attained by females (*re* table 3). Whether or not both sexes have equivalent life expectancies poses still another argument that would have to be reconciled. But, to obviate undue complexity and because breakdown of recapture data by sex

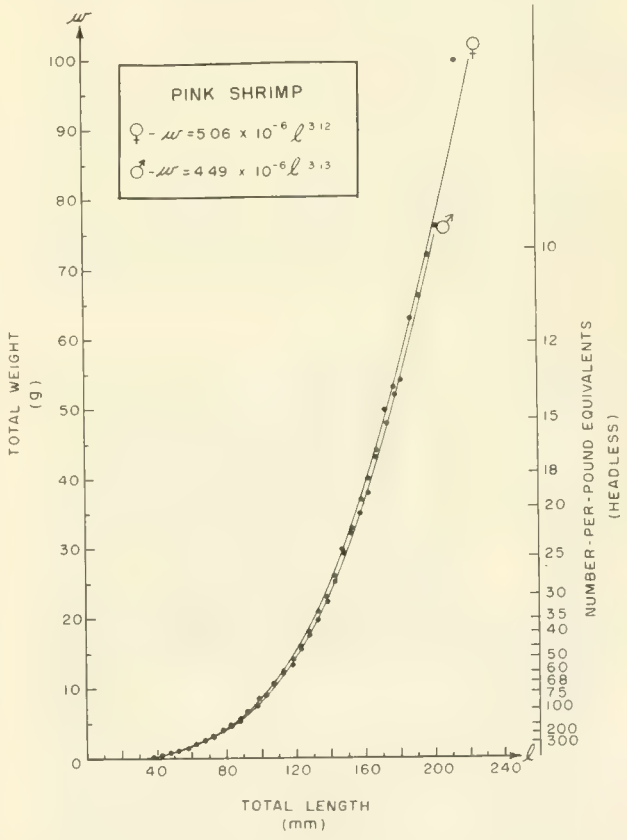


FIGURE 8.—Total weight-total length relationship in pink shrimp.

would have resulted in diminished reliability of sample length and weight estimates, each growth statistic hereinafter computed and substituted in yield equations reflects a compromise or "sexes-combined" situation. Although such statistics are in a sense artificial, their use is justified in that they define the average growth pattern within the experimental population during that period when the age group represented was enjoying greatest biomass, was most accessible, and its sex ratio had not yet begun to indicate a preponderance of females. Each estimate obtained may be viewed as lying intermediate between some upper value for females and a lower value for males.

It follows also that experimental length and weight data from a sexually heterogeneous population yield the most reliable growth-parameter estimates when the sex ratio of marked recaptures remains constant throughout the experiment. In the case of the Tortugas experiment, the sampling distribution of ratios generated over the period t_1-t_8 revealed no significant statistical departure when checked for goodness of fit against the uniform distribution theorized from the sex ratio established at the experiment's beginning [$\chi^2=12.15$ compared with $\chi^2_{.05}$ (6 degrees of freedom)$=12.59$].

TABLE 4.—*Mean lengths and weights of marked pink shrimp recaptured during successive weeks of the Tortugas experiment, September–December 1961 (sexes combined)*

Week of experiment t_i	Number recaptured[1] n	Distribution of males	Mean total length l	Mean weight w	Range in weight	Equivalent number per pound (headless)
		Percent	*Mm.*	*G.*	*G.*	
0	[2] 325	60	88.8	5.9	4.9–6.6	123
1	68	51	90.0	6.1	4.9–7.1	119
2	39	54	92.5	6.6	5.5–8.3	110
3	15	47	103.9	9.5	8.0–10.2	76
4	11	61	106.0	10.2	8.1–11.3	71
5	176	55	109.8	11.4	7.5–15.8	64
6	35	42	113.1	12.5	10.1–18.3	58
7	22	67	118.7	14.5	9.6–17.6	50
8	6	67	123.2	16.2	13.4–19.2	45
9	[3] 1	100	123.4	16.4		44
10	0					
11	0					
12	[4] 2	50	130.4	19.5	18.7–20.2	37

[1] Total number of recaptures used for growth computation. 425 does not agree with total number recaptured during experiment (442) because breakage or other damage precluded carapace-length measurement in some 20 specimens.

[2] Data from 47 recaptures combined with sample data (table 1) secured during period of release.

[3] Measurement from this specimen excluded from growth computation.

[4] One other specimen, 20, returned 3 months after recapture was not included in analysis.

Although comparable growth data contributed by the Sanibel experiment did not meet the requirement of constant sex ratio (table 5), their greater temporal range gave a better indication of the probable shape of the pink shrimp growth curve. Subsequent plots of mean weights of marked shrimp recaptured during successive time increments within each experiment suggested that von Bertalanffy's (1938) growth-in-weight equation offered, as it has in a wide variety of species, the most meaningful and at the same time the most practical solution to the problem of mathematically characterizing shrimp growth (fig. 9). In addition to the exponent b, which is obtained from the weight-length relationship, the function itself,

$$w_t=W_\infty(1-e^{-K(t-t'_0)})^b,$$

contains three parameters that are presumed effectively constant when describing growth over the greater part of the shrimp's life span. W_∞ represents the asymptotic or maximum weight attained by the average shrimp; K is a coefficient proportional to the rate of catabolism; and t'_0 defines a hypothetical age at which the shrimp's weight would have been zero had its growth pattern always been the same as that suggested by the experimental data.[5] If growth be assumed isometric, then b takes the value 3; in the present case, the estimated value, 3.14, was employed. For more extensive discussions on the rationale underlying the von Bertalanffy equation and the advantages that render it particularly adaptable

TABLE 5.—*Mean lengths and weights of marked pink shrimp recaptured during successive 4-week periods of the Sanibel experiment, December 1960–June 1961 (sexes combined)*

Month of experiment t_i	Number recaptured n	Distribution of males	Mean length l	Mean weight w	Range in weight	Equivalent number per pound (headless)
		Percent	*Mm*	*G.*	*G.*	
0	[1] 463	46	75.3	3.5	1.8–8.9	207
1	[2] 1	0	111.7	12.1		59
2	4	100	109.1	11.0	8.2–13.8	66
3	39	38	117.5	14.1	7.1–24.8	52
4	65	52	123.0	16.3	8.1–29.5	44
5	38	39	136.1	22.5	14.4–40.2	32
6	6	33	145.8	27.7	21.9–32.5	26
7	[2] 1	0	157.5	35.2		21

[1] Indicates number of specimens sampled to determine mean length and weight of marked shrimp at start of experiment.

[2] Data from single recaptures not used in growth computation. One additional specimen (20) recaptured in 12th month was also disregarded

To remind the reader that the estimation of growth parameters from mark-recapture experiments necessarily involves the translocation of size and time axes, the notation t_i herein replaces the standard t. The latter represents the true population parameter which may be most accurately estimated only when a reasonably complete series of weight-at-age data for a given species is available. For all practical purposes, it is assumed that the difference between t_i and t, or bias, is negligible.

Throughout this paper, the symbols e and ln designate, respectively, the base of, and abbreviation for, the natural or Naperian logarithm.

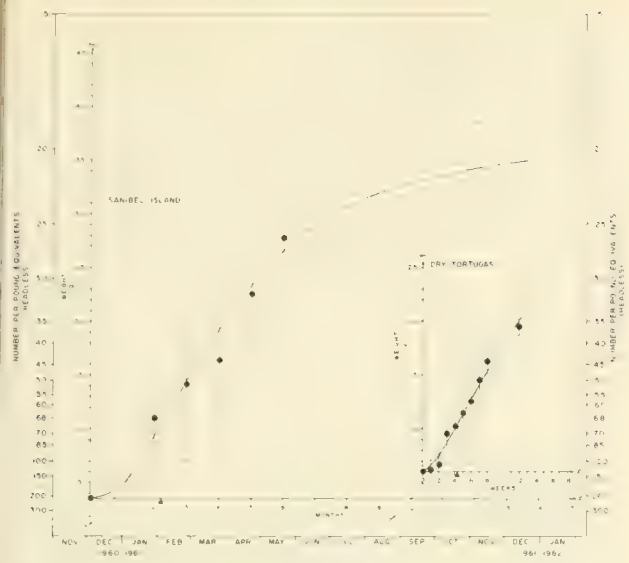


FIGURE 9.—Growth in weight of pink shrimp. Curves are fitted to mean weights of marked shrimp recaptured during successive time intervals of the Tortugas and Sanibel experiments (sexes combined). [Open circles indicate weights of single recaptures not used to fit curves.]

to incorporation in theoretical population models, the reader is referred to the works of von Bertalanffy (1957), Beverton and Holt (1957), Ricker (1958), and Tomlinson and Abramson (1961).

Approximations to W_∞ were obtained by first transforming the von Bertalanffy equation to a form linear in $w_t^{1/b}$ and then fitting the linear regression of $w_{t+1}^{1/b}$ on $w_t^{1/b}$. The intersection of the resulting line with that of proportionality yielded, upon retransformation, the desired estimates (Beverton and Holt, 1957, p. 283). In effect, the intersect signifies the approximate weight at which the ratio of successive growth increments reaches unity, i.e., growth is arrested and maximum weight is attained. The slope of the regression line provides an estimate of e^{-K}.

A distinct disadvantage of this method when working with data from mark-recapture experiments is the requirement that weights be obtained for every one of a reasonably wide range of successive, equal-width time intervals. Unfortunately, W_∞ is quite sensitive to changes in the slope of the fitted line and therefore has real meaning only when the marked population that yielded the data was at all times completely vulnerable to the sampling (fishing) gear, the sex ratio of recaptures remained static, and the resulting mean sample weights display consistent as well as good reliability. Thus, its estimation from the somewhat inadequate Sanibel data had to rely on but four pairs of values (from t_2—t_6), whereas that from the superior Tortugas data was substantiated by seven pairs (from t_1—t_8). Because of considerably less variation about the fitted line, the estimate derived from the Tortugas data is regarded the more stable, and hence the more meaningful of the two (table 6). When estimating W_∞, there was no suggestion in the case of the Tortugas data, and only faint evidence in the Sanibel data, that the fishing gear in general use was selective for faster-growing individuals during the early stages of either experiment.

TABLE 6.—*Pink shrimp growth statistics computed from mean weights of marked shrimp recaptured during successive time intervals of the Tortugas and Sanibel experiments (sexes combined)*

Experiment	Season	Duration	Width of experimental time interval, t	W_∞	K	t_0
		Weeks	*Weeks*	*G.*		*Weeks*
Tortugas	Sept.–Dec.	12	1	[1] 42.0	0.071	0.68
Sanibel	Dec.–June	32	4	35.6	0.339	3.20

[1] Equivalent to a size of 17 headless-count.

After adjusting w_t and W_∞ to unity at the beginning (t_0) of each series of data, the slope of the linear relationship

$$\ln (W_\infty^{1/b} - w_t^{1/b}) = \{\ln (W_\infty^{1/b}) + Kt_0'\} - Kt$$

provided estimates of K, and the ordinate at which the regression line intersects $\ln W_\infty^{1/b}$ gave estimates of t_0' (table 6). Substituting these in the von Bertalanffy equation, theoretical values for w_t were calculated and ultimately defined the curves depicted in figure 9. It is assumed that the values for the constant t_0', although based on data of weight at undetermined age, would have compared reasonably well with those obtained had the actual (rather than the relative) age at each t_t been known.

From table 6 and figure 9, it may be concluded that the results of both experiments are in large degree mutually corroborative. With the Tortugas results arbitrarily established (on statistical grounds) as the standard for comparison, W_∞ is of the same relative order of magnitude while the

growth indices, K, agree surprisingly well (comparative K from the Sanibel experiment=0.339/4=0.085). Weekly growth during the Tortugas experiment averaged roughly 1.5 g. in terms of weight and about 3.4 mm. in terms of total length. From a commercial fisherman's viewpoint, the experimental data (table 4) reveal that it took 12 weeks for the average shrimp to increase in size from 123 to 37 count (headless). Observe also that the minimum commercial size (70 headless-count) in the marked populations was attained about 9 weeks following the start of the Sanibel experiment, and 4½ weeks after the Tortugas experiment began.

AGE AT RECRUITMENT—MAXIMUM AGE

If, as Beverton and Holt (1957) argue, biological rather than mere empirical significance be attached to von Bertalanffy's equation and, further, if the growth pattern as fixed by the constants computed earlier be assumed reasonably typical of pre- as well as postrecruit development, then extrapolation of the curves in figure 9 to the left of t_0 should provide a rough index to the actual ("average") age of shrimp making up each experimental population at the time it was established. Adding this to the time lapsing between an experiment's initiation and the attainment of minimum commercial size by its elements gives a measure of age at recruitment. Fear that the von Bertalanffy equation may not adequately describe growth during the shrimp's earliest developmental stages should not deter pursuit of such an index. No better approach to solving the vexatious problem of age determination in commercial Penaeidae has yet been developed.

In treating accordingly the results of the Tortugas experiment (upon which all subsequent analyses and discussions will be based), a value between 10 and 11 weeks was indicated as the probable age of shrimp released at the experiment's start. When this value is extended by the 4½ weeks the marked shrimp required to reach minimum commercial size, an approximation of 15 weeks for their age at recruitment is obtained. Despite the likelihood that this value may not be too precise, its order of magnitude is quite reasonable in view of what has been observed in a species closely related to (and often occurring with) the pink shrimp, viz., the brown shrimp.

Along the Texas-Louisiana Gulf coast and with little year-to-year variation in chronology, heightened spawning activity in offshore brown shrimp populations during February and March normally results in large masses of postlarvae entering adjacent estuaries during mid-March to mid-April. Present studies by personnel at the Bureau of Commercial Fisheries Biological Laboratory in Galveston, Tex., are yielding good evidence that brown shrimp postlarvae, 8 to 12 mm. long when they reach the barrier island passes, are on the order of 3 to 4 weeks old.[6] Once in inshore waters they grow very rapidly and begin their seaward migration about mid-June as subadults of a size just below the 70-count minimum established above. Thus, the total lapse in time between hatching and attainment of 70-count size (about 10.5 g.) is roughly 15 weeks, which agrees very well with the value obtained for pink shrimp from the Tortugas experiment.

One other growth-associated feature of pink shrimp life history about which the yield equation employed in a later section requires information is the maximum age, on the average, that this species attains. For the common Penaeidae, it has been generally assumed on empirical grounds that 18 months (78 weeks) is a good approximation thereto (Kutkuhn, 1962). Recent analyses of weight frequency distributions in commercial pink shrimp landings indicate, however, that the lapse between an age group's recruitment and its disappearance from the fishery (i.e., its fishable life span) averages about 68 weeks (Kutkuhn, 1962). Hence, upon combining this value with that of the species' average age at recruitment calculated above, a value of 83 weeks, believed to be a better estimate of maximum age, is obtained.

ESTIMATION OF MORTALITY

BASIC ASSUMPTIONS

Computationally as well as conceptually, measurement of mortality—especially natural mortality—is without question more intractable than that of growth and therefore makes greater demands on experimental data. Moreover, since the investigator cannot guarantee that the results

[6] Lindner and Anderson (1956) offer supporting documentation in their study of the contemporary white shrimp, *P. setiferus*, whose postlarvae are also estimated to be about the same age when they enter estuaries at comparable sizes.

of even the most carefully executed mark-recapture experiment will satisfy all theoretical requirements, he is forced when attempting such measurement to rely heavily upon certain conditional assumptions that may or may not be warranted.

Potential sources of bias affecting the accuracy of mortality estimates anticipated from data yielded by the Tortugas experiment have already been discussed. To reiterate, assumptions for which reasonable substantiation was given are: (1) No, or only negligible, losses of experimental shrimp due to rough treatment at release, or to predation during and immediately after release; (2) no losses attributable at any time to after-effects of the mark (dye); (3) little if any movement of marked shrimp from the range of effective fishing during the experiment; and (4) negligible loss of recaptured shrimp because of failure to report them. Information indicating the percentage loss due to nondetection was not obtained, but the manner in which commercial catches were processed leaves little doubt that the likelihood of detecting marked shrimp was high (as was the incentive to do so). Nevertheless, a necessary assumption is that not only was the number of recaptured but undetected shrimp low, but that the ratio of undetected to detected recaptures did not change during the experiment.

THEORY AND EXPERIMENTAL RESULTS

All present-day theory constituting the framework of what is commonly termed "population dynamics" has as its point of departure the concept that the average rate of decline in any population (fish, shellfish, etc.) is at every instant proportional to population size. This relationship may be simply expressed by the differential equation

$$\frac{dN}{dt}=-ZN$$

which, upon integration, gives the geometric progression

$$N_t=N_0e^{-Zt} \qquad (1)$$

with common ratio e^{-Z}, N_0 the initial population size, and N_t the number in the population during any of a series of equal-width time intervals t. Two parameters, N_0 and Z, characterize the expression, with the coefficient Z referred to as the instantaneous rate of total mortality.

The foregoing theorem proves particularly useful in mark-recapture work since the initial size of a marked population, N_0, is almost always known. In some situations this feature readily permits the separation of Z into its components, viz., (1) mortality in the experimental population due to recapture (fishing), and (2) losses of marked members due to all other causes. These quantities are symbolized in the following analysis by the notation F and X, respectively (Beverton and Holt, 1957). Of major interest is the coefficient X, part of which represents true natural mortality, hereinafter denoted by the symbol M. Depending on the acceptability of assumptions concerning the degree to which marked members are not prone to loss other than through fishing and natural mortality, X itself can provide a reasonable approximation of M.

As revealed earlier (fig. 5), the probability of a marked shrimp being recaptured varied widely during the Tortugas experiment. It follows that the corresponding fishing mortality fluctuated accordingly, and that the effects of nonuniform recapture effort would therefore have to be eliminated before attempting to measure total mortality, Z, and, ultimately, natural mortality, M. Two approaches to the satisfactory measurement of Z with recapture data generated under such circumstances are employed herein, whereas only a single alternative offered itself as a solution to the more difficult problem of estimating X (i.e., M).

The first of the two methods used to determine Z entailed application of an analytical method developed for the simple situation where fishing effort (or intensity) does not change appreciably during an experiment. Its use here initially required that, rather than assume within each equal-width time interval a fixed but, between intervals, a successively different (i.e., a discontinuous) fishing mortality, the number of recaptures accumulating in every time interval be adjusted to a continuously uniform fishing effort throughout the experiment (table 7). Such an approach clearly infers that had a static fishing effort prevailed, the pattern of population decline expressed by theorem (1)—with all bias constant or negligible—would have been reflected. In other words, removing the confounding effects of a varying fishing effort served to eliminate all but that part of the overall recapture probability that would

have diminished predictably as the experimental population declined. It is noteworthy that adjustment of each value in the recapture time-series under discussion here was itself independent of time, and hence did not superimpose additional bias whose presence might further curtail the usefulness of mortality coefficients to be estimated by regression techniques from data already serially correlated.

Since it was derived specifically to cover the general case where fishing effort varies throughout an experiment, the second method, which yielded estimates of X as well as Z, did not necessitate any preliminary adjustment of raw data. In large degree, measurements of Z by both techniques proved mutually confirmatory.

TABLE 7.—*Unadjusted and adjusted numbers of marked pink shrimp recaptured during successive weeks of the Tortugas experiment, September–December 1961*

[Number liberated (N_0)=2,090]

Week of experiment	Number recaptured	Distribution of males	Estimated total fishing effort [1]	Number recaptured per 1,000 hours' fishing effort	Log adjusted number recaptured
t_i	n		f	n'	$\ln n'$
		Percent	*Thousands of hours*		
0	47	55	2.11±0.23	22.3	3.105
1	68	51	2.80±0.52	24.3	3.190
2	44	54	3.98±0.30	11.1	2.407
3	15	47	2.82±0.30	5.3	1.670
4	14	61	0.92±0.11	15.2	2.721
5	184	55	3.78±0.20	48.7	3.886
6	37	42	4.04±0.43	9.2	2.219
7	24	67	5.83±0.47	4.1	1.411
8	6	67	10.07±0.62	0.6	−0.511
9	1	100	5.43±0.43	0.2	−1.609
10	0		6.98±0.73	0.0	
11	0		8.92±0.65	0.0	
12	3	33	9.14±0.48	0.3	−1.204

[1] 0.80 confidence intervals.

Subdivision of the Experiment

Preparatory to mortality estimation, plots of the adjusted Tortugas recapture data revealed a distinct but not unexpected discontinuity in the pattern of exploitation during the experiment (fig. 10). Prior to its fifth week, in which most members reached a size acknowledged to be the commercial minimum, the experimental population experienced a measurable amount of purposively selective fishing. Not until the beginning of the experiment's sixth week can it be presumed that recruitment to the "commercial" population was effectively complete. Most interest attaches to the experiment's second phase since estimates of fishing mortality between the points of complete recruitment to and virtual disappearance of

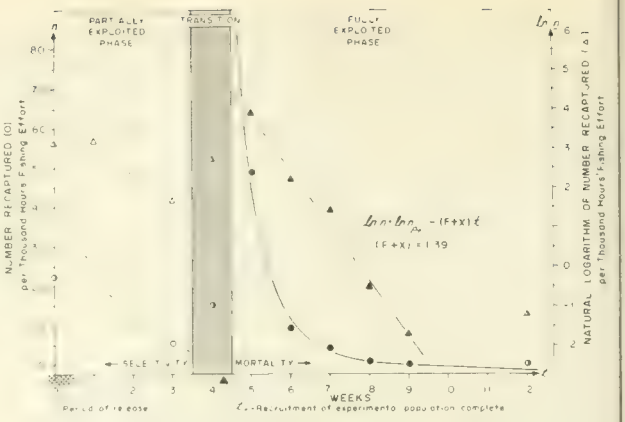


FIGURE 10.—Mortality of pink shrimp. Curves are fitted to numbers of marked shrimp recaptured during successive weeks of the Tortugas experiment (September–December 1961) and adjusted for nonuniform fishing effort. [Number liberated (N_0)=2,090.]

the marked population from the fishery (i.e., from t_5 to t_{10}), and natural mortality just prior to and over the same period (i.e., from t_4 to t_{10}), are included among the major objectives of this study.

The experiment may therefore be conveniently subdivided into two phases arbitrarily separated by a brief (1-week) interval of transition. They are: (1) A period in population development when the fishery exercised moderate selectivity—the partially exploited phase, which was characterized by varying degrees of purposive as well as gear selectivity; and (2) a period of nonselectivity—the fully exploited phase, during which every population member was vulnerable to all operating causes of mortality.

Total Mortality During Partially Exploited Phase

Proceeding from theorem (1), which, upon transformation to logarithmic form, becomes linear in $\ln N_t$ and t, Beverton and Holt (1957, pp. 185–191) give in terms of the recaptures themselves a comparable expression intended for use with marked populations subjected to a uniform fishing (recapture) effort. Thus, making appropriate substitutions,

$$\frac{dn}{dt} = FN_t = FN_0 e^{-(F+X)t}$$

and, ultimately,

$$\ln n_2 - \ln n_1 = -(F+X)\tau \qquad (2)$$

where $n_1, n_2, \ldots n_i$ refer to the number of marked individuals recaptured during the first, second, . . . i^{th} time interval t, respectively; $\tau = t_{i+1} - t_i$ ($=1$ week); F and X are the instantaneous coefficients of reduction of marks due, respectively, to fishing and to all causes other than fishing; and $(F+X)=Z$. It follows from expression (2) that a linear regression of the natural logarithms of successive numbers of recaptures on time gives estimates of ln n_1 and Z.

Fitting a regression to the logarithms of Tortugas recaptures grouped by weeks and adjusted for nonuniform fishing effort (viz., ln n_1' through ln n_3', where the prime indicates an adjusted value) yielded an estimate of 0.76 for Z, the only parameter of interest during the experiment's initial phase. Figure 10 shows that the regression enjoyed a good fit.

Obviously, a measurable amount of (selective) fishing effort contributed to the total mortality value so obtained, though by far the greater share of this value is presumed attributable to natural causes. Only a very minor part is believed due to the "other-loss" factors defined earlier. There is moreover, no statistical evidence of any differential vulnerability of sexes during the partially exploited phase. Despite the slower growth noted for males, the sex ratio of recaptures never departed significantly from that observed at the start of the experiment (table 7). In summary, a small amount of fishing activity during the experiment's first phase was sufficient to demonstrate an apparently high corresponding rate of natural mortality, which, as will be shown later, continued well into the second or fully exploited phase. Here it became associated with the relatively high rate of fishing mortality established at the moment recruitment was completed.

Mortality During Fully Exploited Phase

After plotting the logarithms of the adjusted numbers of shrimp recaptured during the first 5 weeks of the Tortugas experiment's fully exploited phase, and observing that they, too, all fell nearly in a straight line (fig. 10), computation of their linear regression on time [equation (2)] gave a first estimate of $Z=1.39$ for the instantaneous coefficient of mark reduction due to all causes.

Attempts to subdivide the resulting Z into its fishing mortality and "other-loss" components proved impractical, however, when recapture data adjusted for varying fishing effort were substituted in techniques implicitly designed for unadjusted data generated by a uniform effort. Inspection of the basic equations involved (Beverton and Holt, 1957, p. 190, equations 14.15 and 14.16) reveals that the soundness of F and X (or M) estimated therewith may be influenced not only by the size of N_0 (or any specified equivalent), but also by variation in the relative magnitude of the antilog of ln n_1 (or its counterpart), where the latter value is derived by means analogous to equation (2). It will be recalled that initial treatment of the recapture data entailed their being grouped on a weekly basis, and then adjusted within each time unit for nonuniformity of fishing effort between units by a factor equal to the reciprocal of the quantity $(f_i \times 10^{-3})$, with f_i representing the overall effort in hours expended on the fishing grounds during the i^{th} weekly interval (table 7). Subsequent difficulty stems from the arbitrary nature of the attenuation index, 10^{-3}, which must be selected so as to yield adjusted recapture values having an average order of magnitude moderately close to that of the unadjusted values.

Whereas analysis of recapture data so adjusted provides [through expression (2)] a good estimate of the total-loss coefficient $Z=(F+X)$, such subjective treatment imparts bias of unknown degree to the values for F and X when these are delineated by the equations mentioned above. This bias will be proportional to the value of n_1 as estimated by expression (2), and, accordingly, to the relative size of the adjustment index employed. The real problem, however, lies in not being able to specify satisfactorily the relationship between N_0 and the estimated initial value of the recapture time-series based upon adjusted data, as contrasted to that between N_0 and the corresponding value of the time-series involving unadjusted data.

Drawing support from the fundamental theorem stating that over a given time interval r, fishing mortality is proportional to fishing effort (or intensity), i.e., $F_r = cf_r$, Beverton and Holt (1957, p. 192) derive solely in terms of recapture and related effort values a useful equation which furnishes—independent of N_0—an estimate of the other-loss coefficient X, regarded herein for the reasons outlined earlier as a close approxima-

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tion of M. This equation is given by

$$\frac{1}{\tau_r}\left[\ln\left(\frac{n_r f_{r+1}}{n_{r+1} f_r}\right) + \ln\left\{\frac{(cf_r+X)(1-e^{-(cf_{r+1}+X)\tau_{r+1}})}{(cf_{r+1}+X)(1-e^{-(cf_r+X)\tau_r})}\right\}\right] = cf_r+X \quad (3)$$

where τ signifies the width (in weekly units) of experimental time intervals r or $r+1$, n identifies the number of recaptures in the same intervals, and c denotes the average coefficient of proportionality relating fishing mortality to fishing effort, f_r.

Equation (3), accounting inherently for varying fishing effort, is linear in f_r and a logarithmic expression (left side) corresponding to the ratios in successive time intervals of the numerical abundance of marked individuals composing the experimental population. Accordingly, simple regression procedures involving at least two iterations lead to fairly good estimates of c and X, the slope and y-intercept, respectively. The latter value may be viewed as a measure of the average total-loss rate that would have prevailed during the experiment in the absence of any fishing activity.

Use of expression (3) assumes that bias introduced by the practical need to treat fishing effort as a discontinuous function of time is negligible. Its application to appropriate recapture data and corresponding values of effective fishing effort gave, after three iterations, estimates of $c=0.171$, $X=0.55$, and average $F=0.96$ for the fully exploited phase of the Tortugas experiment (fig. 11). Interestingly, the resulting value for $Z=(F+X)=1.51$ compared quite favorably with the preliminary value calculated earlier, viz, $Z=1.39$, differing on the order of but 9 percent. Relevant statistics are presented in table 8. Note here the incorporation of effort data slightly modified from those used earlier to obtain the preliminary estimate of Z. The decision to subject to analysis only those measurements of effort expended inside 20 fathoms was prompted by the observation that none of the 252 marked shrimp retrieved during the period of interest (table 8) was recaptured beyond this range. Such adjustment seemed necessary to minimized the likelihood of violating, in terms of the experimental population and that portion of the fishery's overall activity

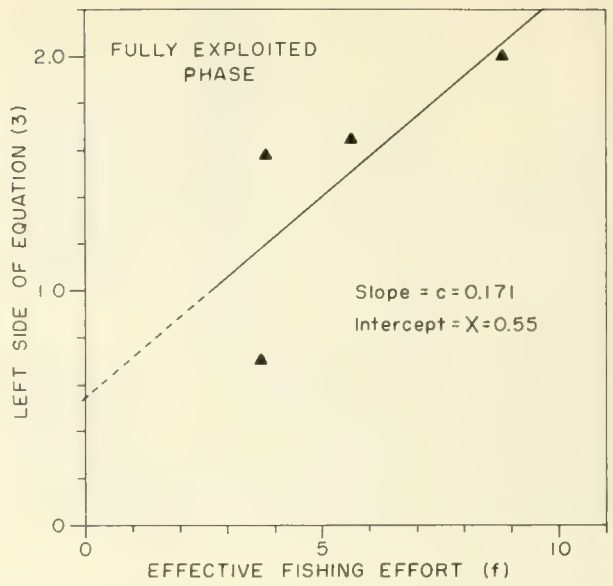

FIGURE 11.—Estimating the other-loss coefficient X using equation (3) of text. [Refer to table 8 for description of data and associated statistics.]

directly associated with it both spatially and temporally, the functional relationship between fishing mortality and fishing effort (or intensity) stated above.

Transformation of estimated F and X to corresponding weekly rates of reduction in marks resulted in values of 0.62 for that due to fishing, and 0.42 for that due to all other causes (see Ricker, 1958, p. 25, for discussion of relationships). These results, while indicative of greater mortality pressure on parent shrimp populations than had

TABLE 8.—*Statistics employed to estimate with equation (3) of text the other-loss coefficient X for the fully exploited phase of the Tortugas experiment*

[Resulting F values are given in the last column; $c=0.171$]

Week of experiment	Rank in time-series	Width of experimental time interval	Number recaptured	Estimated effective fishing effort [1]	Left side of equation (3)	Estimated fishing mortality
t_r	r		n	f		$F=cf$
		Weeks		*Thousands of hours*	Ln *units*	
5-	1	1	184	3.78	1.583	0.65
6-	2	1	37	3.68	0.725	0.63
7-	3	1	24	5.60	1.642	0.96
8-	4	1	6	8.76	1.996	1.50
9–10	5	2	1	11.73		2.01

[1] Treated here is synonymous with *fishing intensity* which, in broader geographical application than is here necessary, is explicitly defined as fishing effort per unit area; data represent only that amount of effort expended on the Tortugas fishing grounds inside the 20-fathom contour (re table 2).

been widely spectulated, are not unreasonable when one considers the species' high reproductive potential, short life expectancy, gregarious habits, and, presumably, its sensitivity to environmental fluctuations. Such characteristics, as they control population development, are not atypical of Arthropoda in general.

Returning to the matter of discontinuity in temporal distribution of recaptures during the Tortugas experiment (table 7, fig. 10), observe now that its further reconciliation is possible. The value obtained for X, 0.55, which is henceforth assumed for the reasons noted earlier to have been practically all due to natural causes, is readily contained in the total-loss coefficients estimated for both partially and fully exploited phases, viz, 0.76 and 1.51, respectively. If natural mortality is presumed to have been effectively constant through the transition period, then the difference in residuals (fishing mortalities, $F=0.21$ versus $F=0.96$) may be immediately attributed to cessation of selective fishing accompanied by an abrupt rise in fishing rate upon completion of recruitment. It appears that had the low rate of recapture established during the partially exploited phase continued, subsequent computations would also have led to an estimate for X (hence M) comparable to that determined from existing data for the fully exploited phase.

That the instantaneous rates of mortality do not remain constant over extended periods of time but diminish with age is suggested by a small number of marked shrimp having been recaptured late in the experiment. Note in figure 10 that their corresponding logarithm fell far to the right of the line fitted to those of adjusted numbers of recaptures made earlier in the experiment.

In summary, the foregoing results are interpreted to reflect exclusively conditions in that age group of shrimp represented by the experimental population, and hence should only be applied with great caution in other fisheries, or to other age groups at different seasons. Every age group (as herein defined) is but one of a succession of groups that may overlap several seasons. Each is therefore likely to be subjected at every stage of development to different levels of exploitation as well as to changing ecological conditions, with the high expectation that mortality parameters will vary accordingly.

YIELD IN WEIGHT AS A FUNCTION OF AGE (SIZE) AT RECRUITMENT

To answer the fundamental question posed earlier, it remains now to express the interaction of population growth and mortality in terms of expected yield when age (or size) at recruitment is varied over a wide range of values. Thus, so that the commercial return from a particular age group (or, in general, all age groups combined) will be maximal, at what average age of shrimp, under the conditions of observed growth and mortality, should harvesting begin?

THEORETICAL POPULATION MODEL

A satisfactory answer may be provided through application of any one of several mathematical population models, or analogs, which have been developed to facilitate study of the dynamics of open, self-maintaining biological systems (e.g., Watt, 1956; Beverton and Holt, 1957; Ricker, 1958). Notwithstanding its possible shortcomings, all of which are thoroughly discussed at appropriate stages in its derivation, the simple model developed and applied by Beverton and Holt (1957, pp. 35–38 and 309–327) was chosen for the purposes of this study because it offered the most straightforward solution to a practical problem.

Deterministic in nature, i.e., growth and mortality are presumed effectively constant from recruitment onward to the end of the species fishable life span, the expression for the shrimp population's mean weekly biomass over this period is given by

$$\bar{P}'_W = Re^{-M\rho}W_\infty \sum_{n=0}^{3} \frac{\Omega_n e^{-nK(t_{\rho'}-t_0)}}{F+M+nK}\ (1-e^{-(F+M+nK)\lambda})$$

where F and M are, respectively, the coefficients of instantaneous fishing and natural mortality; W_∞, K, and t'_0 are the growth parameters defined earlier; R represents the number of shrimp recruited weekly to the fished population; $t_{\rho'}$ is the age, corresponding to the minimum commercial size referred to above, at which recruitment is no longer influenced by selective fishing; $\lambda=t_\lambda-t_{\rho'}$ indicates the population's fishable life span (t_λ being the species mean life expectancy); and $\rho=t_{\rho'}-t_\rho$ designates an interval during which some recruitment occurs because of selective fishing but population decline is mainly attributable to natural causes (t_ρ indicating the age at

which shrimp become liable to selective capture but, generally speaking, have not yet attained commercial acceptability). In practice, for a given set of conditions, ρ is usually negligible and $t_{\rho'}$ and t_ρ may be considered equivalent. The remaining notation arises from the need, during the model's development, to expand the exponential term of the von Bertalanffy growth equation.

Thus, if we let $b=3$,

$$w_t=W_\infty(1-e^{-K(t-t_0')})^b$$

may be algebraically transformed to

$$w_t=W_\infty\sum_{n=0}^{3}\Omega_n e^{-nK(t-t_0')}$$

where the appropriate coefficients of the binomial expansion are

$$\Omega_0=+1,\ \Omega_1=-3,\ \Omega_2=+3,\ \Omega_3=-1$$

with n taking the values 0, 1, 2, and 3. Although earlier analysis of the weight-length relationship suggested that growth in pink shrimp is not truly isometric, use of the foregoing model assumes, for practical purposes, that it is. Actually, the minor effects of a departure from isometry should be taken into account by appropriately varying W_∞, but failure to do so here does not lessen the validity of later findings.

From the biomass equation just postulated, it follows that an expression for the mean weekly yield of the fished population may be represented by

$$Y_W=F\bar{P}_W'.$$

And since R, the recruitment, is the only one of the parameters describing $\bar{P}_W'$ that is not ordinarily amenable to measurement, further modification results in

$$\frac{Y_W}{R}=\frac{F\bar{P}_W'}{R}=Fe^{-M\rho}W_\infty\sum_{n=0}^{3}\frac{\Omega_n e^{-nK(t_{\rho'}-t_0')}}{F+M+nK}(1-e^{-(F+M+nK)\lambda}) \quad (4)$$

hereinafter referred to as the expected yield in weight per recruit.

DETERMINATION OF YIELD MAXIMUMS

By varying $t_{\rho'}$, and hence ρ and λ, curves of yield as a function of age can be generated with equation (4) for fixed values of the remaining parameters. The process obviously entails prior establishment of some absolute minimum value for t_ρ, this value corresponding in subsequent analyses to a size below which all shrimp are not only commercially unacceptable, but also incompletely vulnerable to the gear in common use.

Yield Curve for Observed Parameter Values

We have, from the Tortugas experiment and other sources, the following values for the indicated parameters:

$M=0.55$ $\quad t_0'=0.68$ week

$F=0.96$ $\quad t_\lambda=83$ weeks

$K=0.07$ $\quad t_\rho=15$ weeks [7]

$W_\infty=42.0$ g.

Recall also that $\lambda=t_\lambda-t_{\rho'}$ and $\rho=t_{\rho'}-t_\rho$. Substituting these in equation (4) and solving it for each of not less than nine carefully spaced values of $t_{\rho'}$, the yield curve farthest to the left in figure 12 was obtained. It is immediately apparent from this figure that in a population whose development is governed by growth and natural mortality of the magnitude observed for the Tortugas pink shrimp population, peak biomass is attained somewhat before, rather than after, the average shrimp reaches a size equivalent to the present commercial minimum. Growth, although relatively high in contrast to that determined for a variety of species supporting other commercial fisheries, evidently cannot compensate (to man's economic advantage) for losses accruing to a high natural mortality. Nor is postponement of full-scale exploitation indicated unless reduced environmental effects can be expected to result in a markedly lower natural mortality. Under observed conditions, delaying exploitation until the shrimp reach a greater initial size would indeed result in a negligible gain in yields of so-called premium shrimp, but only at the expense of a significant reduction in the total yield of all sizes.

Yield Curves Theorizing Lower Levels of Natural Mortality

Of the parameter estimates obtained in this study, by far the firmer and at the same time the least subject to wide temporal variation are those

[7] Age roughly corresponding to the minimum commercial size of 70 headless-count.

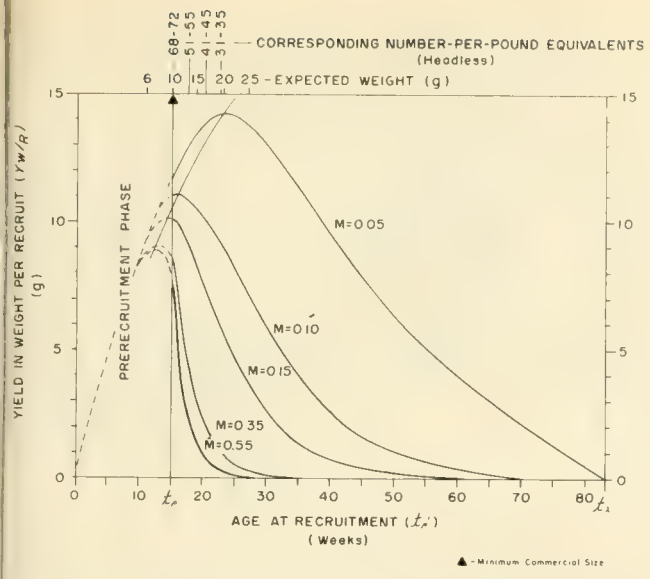

FIGURE 12.—Yield in weight per recruit against age at recruitment for different levels of natural mortality (M) in a population of pink shrimp. [$F=0$; 96, $K=0.07$; $W_\infty=42.0$ g.; ▲ indicates an observed as contrasted to a hypothetical value.]

describing growth. In contrast, greater variation would be expected for natural mortality since it may be readily conceived as the more sensitive to and hence the more likely of the density-dependent parameters to reflect even the most subtle of environmental vagaries. In other words the potentialities for growth in the individual are largely predetermined within rather narrow limits by the characteristics of the species; those for natural mortality, which are enhanced through great prolificness, largely by the environment.

With this in mind, additional curves were generated in like manner for four hypothetical and successively lower values of the natural mortality coefficient (fig. 12). These illustrate very clearly what happens when, with respect to some economic standard t_p, natural mortality becomes increasingly compatible with growth. For any magnitude of exploitation (F), maximum yields will always occur at higher levels and at more advanced recruitment ages as natural mortality establishes itself at lower and lower levels. Under the growth restrictions imposed here, postponing initiation of exploitation would not be justified unless the observed natural mortality rate were on the order of 0.10 or less. It may be argued now that even if the observed value for M (0.55) constituted a gross overestimate of the true natural mortality, the associated error would have had to be rather large before the general conclusion just reached could be viewed with suspicion. The present example also shows that with a natural mortality of 0.05 (which is untenably low for shrimp), the highest yield is obtained when age at recruitment is increased to about 23 weeks, this corresponding to a shrimp size of roughly 31–35, headless-count. Dashed portions to the left of t_p arbitrarily designate the likely order and shape of the yield curves for that part of the hypothetical population not yet possessing economic worth.

Effects of Variation in Rates of Growth and Exploitation

To illustrate how changes in the critical factors of growth and fishing mortality influence the yield curve's shape and the position of its maximum point, curves for selected (hypothetical) parameter values are compared with those derived above for observed values. If yield is described as a function of age at recruitment for varying rates of growth (fig. 13A), it will be noted that the effect of a higher rate of growth than that observed is an increase in amplitude of the yield curve and a shift in its maximum point to the left, with whatever recruitment size is designated as the standard minimum remaining the same as before. In other words, every shrimp reaches the smallest acceptable size at an earlier age. Conversely, at a given level of natural mortality, a lower rate of growth tends to decrease curve amplitude and move the point of maximum yield to the right, the minimum marketable size again remaining fixed but being attained at a later age.

Exercising care to judge each new set of conditions on its own merits, it appears that increased rates of growth such as postulated in figure 13A would still not be sufficient to justify any advance of recruitment age where a high natural mortality prevails. At a low mortality level, an advance of recruitment age is indicated only when concurrent growth is also of a low order. Hence, for a fixed natural mortality, successively higher rates of growth would merely dictate a retrogression in recruitment age (but not size) if maximum yield is to be achieved. This relationship implies no change in minimum acceptable size at recruitment but, instead, as in the observed situation where low growth rate complements high natural mortality, a greater overall yield by the age group involved during its fishable life span.

By comparison, changes in the level of fishing may be expected to produce only relatively minor differences in both the position and height of yield curve maximums (fig. 13B). The revelation that the magnitude of fishing (F) is actually of little concern when deciding at what age or size to begin harvesting a resource in order to achieve maximum yields should not create the impression that fishing mortality has no significance at all. Although maximum utilization of a domestic shrimp resource is the issue under discussion here, the fact remains that resource maintenance is still the overriding objective of shrimp research. As pointed out earlier, the matter of recruitment age or size is at this point largely one of economics. Yet to be answered is the question of how much (in contrast to what size) shrimp may be harvested and still have sufficient residual to maintain the resource at the highest level consistent with projected environmental conditions. In effect, rather than inquiring as to the optimum $t_{p'}$, we should perhaps be asking: What is the optimum F?

Employing commercial fishery statistics, a prior analysis of the Tortugas pink shrimp stock gave rise to speculation that a decline in production over the period 1956–59 was attributable more to poor utilization of supplies than to too intensive fishing and hence improper maintenance of the stock (Kutkuhn, 1962). The observation was made that increasingly heavy exploitation of new recruits, as they enter the fishing grounds and before their average growth rate reaches a maximum, appeared to have systematically reduced annual biomass. Although this conclusion seems to be in conflict with the findings of the present study, it must be stressed that the earlier analysis was necessarily cursory due to certain data inadequacies and that it attempted to generalize over a long period of time and a variety of conditions. In contrast, the results reported here represent a well-organized effort to acquire the information needed to answer specifically the question posed. They are therefore quite explicit where the others were not, and, accordingly, merit much greater attention and could even be put to interim use.

The present findings do not, however, constitute the final solution to the stated question. As did those of the first analysis, they only reflect the accumulation of more and better data, and merely serve as one of several anticipated stepping stones toward an unassailable objective.

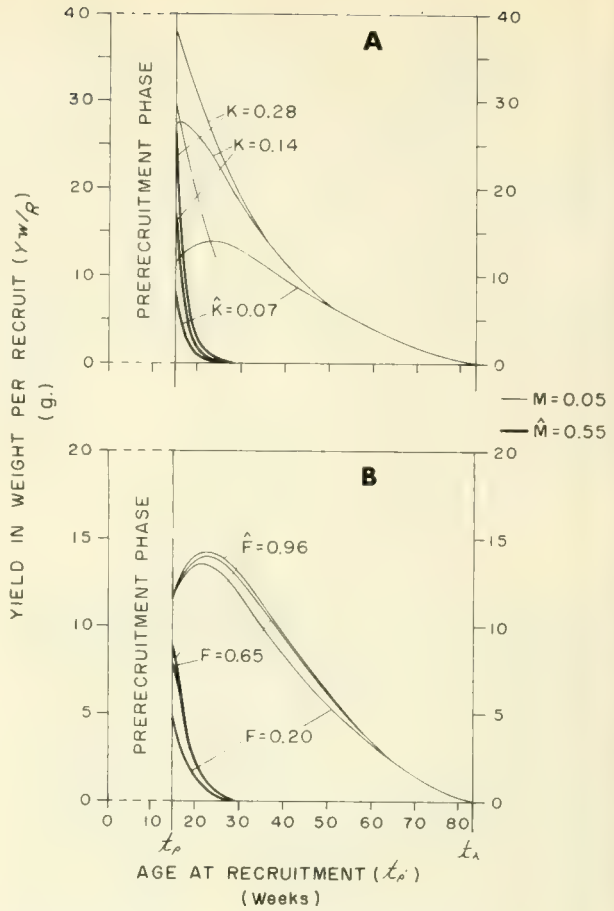

FIGURE 13.—Yield in weight per recruit against age at recruitment for observed and hypothetical levels of growth (K), fishing mortality (F), and natural mortality (M) in a population of pink shrimp. [In plate A, $F = 0.96$, $W_\infty = 42.0$ g., and the ordinate through $t_p = 15$ weeks refers, in terms of corresponding shrimp size, only to the curves for $K = 0.07$; in plate B, $K = 0.07$ and $W_\infty = 42.0$ g.; ▲ indicates an observed value.]

YIELD IN VALUE AS A FUNCTION OF AGE (SIZE) AT RECRUITMENT

Perhaps more meaningful to the entrepreneur is an indication of the size at which harvesting should commence so that total shrimp production will enjoy highest possible value. Necessitated by consumer demands, a well-known characteristic of the Gulf coast shrimp industry is the gradation of ex-vessel price according to the size of shrimp landed and sold. Knowledge of the price-size relationship may be used to advantage in determining where, in different growth and mortality

situations, the curve of yield value on recruitment age reaches a maximum.

VALUE IN RELATION TO SIZE

For the purposes of this study, particular attention was given the price structure for pink shrimp landed at Key West, Fla., during the Tortugas experiment, September to December 1961 (table 9). A plot of mean price on whole-weight equivalents for each of 11 size (headless-count) categories suggested that price could be treated as a logarithmic function of weight (fig. 14). The empirical relationship proved to be satisfactorily described by an equation of the form

$$p = a + b \ln [\ln w], \qquad w \lessapprox 10$$

where p signifies the price per pound, w is the corresponding weight on an individual-shrimp basis, and a and b denote constants. Note that the expression has been rendered discontinuous at a shrimp weight of slightly more than 10 g., which corresponds to the minimum commercial size of 70 headless-count recognized earlier, and which commanded the lowest price then in effect (fig. 14). Dealers accepting them paid the prevailing minimum rate (30 cents per pound) for all smaller shrimp.

Having established a reasonably acceptable expression for the basic relationship between market price and individual shrimp weight, it was then possible to develop one relating the latter variable to corresponding shrimp value (fig. 14). Data generated in the process served the needs of subsequent analyses.

VALUE AS A FUNCTION OF TIME

Since shrimp value increases predictably with weight, a corollary is that it behaves similarly with respect to time. Thus, simple transformation of weight to value units results in a temporal distribution of points which may be empirically defined by the growth equation employed in a previous section. By treating the Tortugas experimental data (table 4) accordingly, estimates of the constants in the regression of value on time were computed. The counterparts of W_∞ and K, respectively, $V_\infty = 4.8$ cents approximated the shrimp's maximum attainable value, and $K_v = 0.08$ represented an index of the rate of value decrease; t_0', remained fixed at 0.68 week, the value employed above in the description of growth in weight. When fitted to the experimental observations, the resulting expression for shrimp weight in terms of value as a function of time yielded a curve over the range of values 0.5 to 5.0 cents (per shrimp) closely comparable to that given by the corresponding expression for growth in weight.

DETERMINATION OF YIELD-IN-VALUE MAXIMUMS

After appropriate substitutions were made for the above growth-in-value constants, solution of equation (4) for various recruitment ages ($t_{p'}$) at each of four levels of natural mortality (M) permitted construction of the desired yield-in-value

TABLE 9.—*Weekly ex-vessel prices paid for pink shrimp landed at Key West, Fla., 1961*

[Values are in cents per pound for headless shrimp graded by sample (box) count] [1]

Week ending	Size category (Number per pound—headless)									
	68–72	61–67	56–60	51–55	46–50	41–45	36–40	31–35	26–30	21–25	15–20
Sept. 16	32	40	41	50	51	57	59	64	69	74	79
23	31	36	41	46	51	56	61	66	71	76	81
30	27	31	41	46	51	56	61	66	71	76	81
Oct. 7	28	34	41	46	51	56	61	66	71	76	81
14	28	34	41	46	51	56	61	66	71	76	81
21	23	29	36	41	46	51	54	61	66	71	76
28	23	29	36	41	46	51	56	61	66	71	76
Nov. 4	26	32	39	44	49	54	59	64	69	74	79
11	29	35	42	47	51	56	61	65	70	75	80
18	29	35	42	47	51	56	61	65	70	75	80
25	32	38	45	50	54	58	62	67	72	77	82
Dec. 2	32	38	45	50	54	58	62	67	72	77	82
9	32	38	45	50	54	58	62	67	72	77	82
16	32	38	45	50	54	58	62	67	72	77	82
23	32	38	45	50	54	58	62	67	72	77	82
30	34	40	47	52	56	60	64	69	74	79	84
Mean	29 4	35. 3	42. 0	47. 3	51. 5	56. 2	60. 5	65. 5	70. 5	75. 5	80. 5
Whole-weight equivalents (g.)	10. 5	11. 4	12. 6	13. 8	15. 3	17. 0	19. 2	22. 1	26. 1	32. 5	41. 7

[1] Source: Market News Service, Bureau of Commercial Fisheries, U.S. Fish and Wildlife Service.

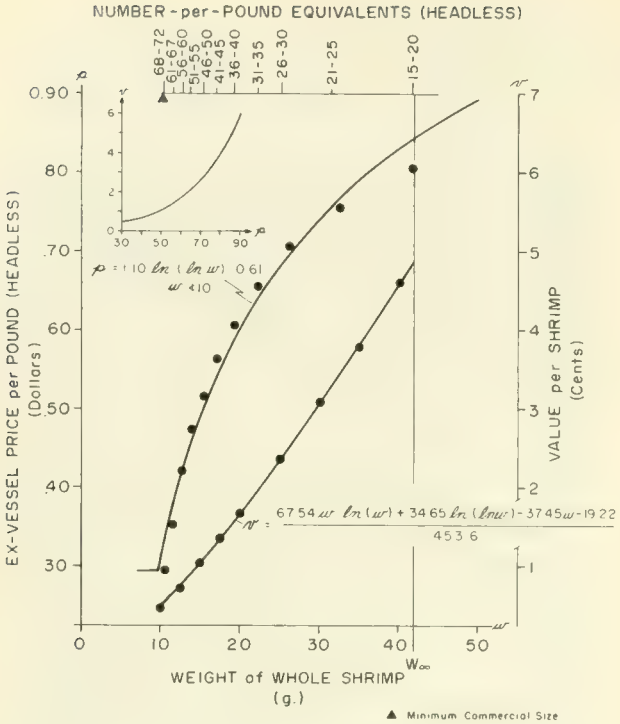

FIGURE 14.—Ex-vessel price (p) against weight (w) of pink shrimp landed at Key West, Fla., during September–December 1961. Also shown are the expression for converting price to value (v) on an individual-shrimp basis, and the resulting plot of value as a function of shrimp weight. In the upper left-hand corner, the value per shrimp in cents is graphed as a function of price per pound in the same units.

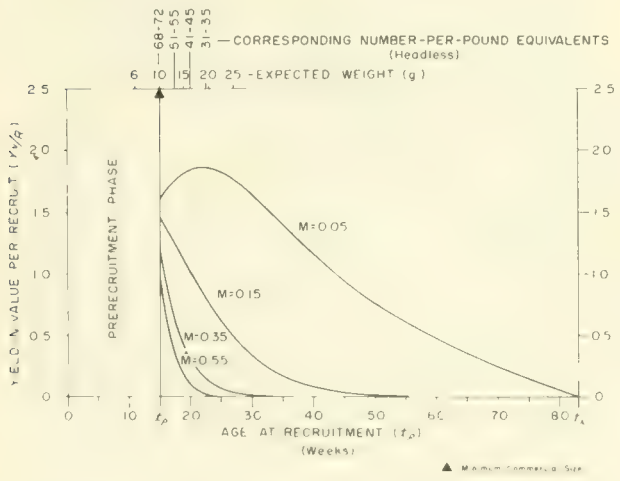

FIGURE 15.—Yield in value per recruit against age at recruitment for different levels of natural mortality in a population of pink shrimp. [$F=0.96$; $K_v=0.08$; $V_\infty=4.8$ cents (per shrimp); ▲ indicates an observed as contrasted to a hypothetical value.]

curves (fig. 15). Upon comparing these with the yield-in-weight curves shown in figure 12, the most noticeable (though not necessarily significant) difference is seen in the relative positions of their maximum points. Unless natural mortality is extremely low, highest economic yield from a given age group during its fishable life span clearly occurs when exploitation begins as soon as the average shrimp attains commercial acceptance. In all but those circumstances where extraordinarily low natural mortality operates, no advancement of the recruitment age is indicated. This implies, of course, that the relationship between price and size holds relatively static.

Of interest is the general observation that, in situations where postponement of exploitation may be in order, maximum economic yield can be expected at a recruitment age (or size) slightly lower than that suggested for maximum biological yield. Figures 12 and 15 for $M=0.05$ illustrate this very nicely. Note that the yield-in-weight curve (fig. 12) reaches its highest point at a recruitment size of about 31–35 count (headless), whereas the yield-in-value maximum occurs roughly at a headless-count somewhere between 36 and 40 (fig. 15). This difference is of appreciable biological magnitude and can be largely attributed to the somewhat higher rate of growth in terms of value ($K_v=0.08$ versus $K=0.07$). To reiterate, at levels of natural mortality known to be well within the range of expectation, the total yield of a given age group during its fishable life span will be maximal only when fishing begins at the minimum marketable size. Postponement to a larger initial size would engender economic loss.

SUMMARY

Measures of growth and mortality in a population of pink shrimp obtained simultaneously by the mark-recapture technique permitted critical examination of the interrelationship of these parameters in assessing present utilization of the resource.

Of 2,090 carefully graded, precommercial-size shrimp injected with blue dye and released in late September (1961) at a point on the periphery of the well-known Tortugas (Florida) fishing grounds, 443 (21 percent) were returned during the ensuing 3 months. Recapture (commercial fishing) effort was closely surveyed throughout this experiment

and then used to remove the effects of its uneven distribution from subsequent mortality estimates. Results of an earlier mark-recapture experiment performed with the same species but in an adjacent area and for a different purpose corroborated growth-parameter estimates from the Tortugas experiment.

After the various metric relationships used to convert length to weight units were documented, the von Bertalanffy growth function was fitted to the mean weights (sexes combined) of marked shrimp recaptured during successive, equal-width time intervals characterizing each experiment. The more meticulously executed Tortugas experiment yielded for the function's parameters the values: $W_\infty=42.0$ g.; $K=0.071$; and $t_0'=0.68$ week. Weekly growth in weight during the rectilinear phase of the observed growth pattern averaged 1.5 g., which corresponded to a length increment of about 3.4 mm. In terms of commercial count size, the average experimental shrimp required 12 weeks to increase in size from 123 to 37 headless-count. Minimum commercial size (70 headless-count) was reached approximately 4½ weeks after the experiment began, and at an estimated age of 15 weeks. The life expectancy of the pink shrimp was assumed on the basis of other studies to be about 83 weeks.

The Tortugas experiment had to be subdivided into partially exploited and fully exploited phases before fishing and natural mortality could be calculated. Rates of total mark-loss during both phases were estimated by regression techniques from recapture data grouped by weeks and adjusted for nonuniform fishing effort. Separation of the value obtained for the fully exploited phase into its fishing and natural mortality components, F and M respectively, proved impractical, however, when attempts were made to apply mathematical procedures designed specifically to accommodate unadjusted recapture data generated by a constant fishing effort. Difficulty arose from an inability to evaluate satisfactorily the absolute size of the experimental population at the start of its fully exploited phase. Subsequent measurement of F and M by a procedure independent of the initial size of the marked population's second phase, and inherently accounting for varying fishing effort throughout, yielded estimates of 0.96 and 0.55 respectively. Their transformation to weekly mortality rates gave the corresponding values 0.62 and 0.42. Notwithstanding statistical limitations, these observations draw attention to the fact that at least in some areas, certain age groups (or broods) of commercial shrimp may be subjected to rather rapid deterioration from artificial as well as natural causes.

After substituting therein observed and hypothetical values for the parameters of growth and mortality, a relatively simple yield equation was solved for each in a series of selected age-at-recruitment values. With 15 weeks (corresponding to a size of 70 headless-count) established as the absolute commercial minimum age and thereby serving as the point of departure, the resulting curves of yield on age at recruitment clearly showed that unless the expected level of natural mortality falls well below that observed, postponement of fishing until shrimp reach a greater initial age (or size) is not justified. Observed growth, although comparatively high, cannot offset concurrent losses due to the substantial natural mortality that seemingly prevails when shrimp availability is at a maximum. Delaying the start of harvesting would subsequently result in slightly greater catches of shrimp in the larger size categories, but only at the expense of an appreciably diminished overall catch.

Even more convincing were the results of a similar analysis in which weight and hence the growth function's parameters were expressed in terms of value. For any level of natural mortality (observing the restriction imposed by the absolute commercial minimum presently in effect), maximum yield in value is attained when fishing commences at a shrimp size perceptibly below that at which maximum yield in weight would be expected.

The questions tentatively answered by this study have far greater implications from an economic than from a biological standpoint. Still of great concern is the problem of resource maintenance. We are unquestionably in a better position to judge when, in the development of any age group, the harvesting of shrimp should begin so as to obtain maximum production therefrom. But it remains for us to evaluate that level of fishing which, for a given set of environmental conditions and for the shrimp resource as a whole, is most conducive to our ultimate objective: maximum equilibrium yield.

ACKNOWLEDGMENTS

The successful outcome of the Tortugas experiment must in large part be attributed to the unstinting efforts of those responsible for its implementation and completion. Acknowledgment is especially due Thomas J. Costello who guided the experiment's marking and recovery phases; credit for assistance in all aspects of the field work is extended to Bureau and industry personnel alike. The author also appreciates the assistance rendered by Charles H. Lyles, Jr. and George W. Snow, Branch of Statistics, who expedited the availability of certain commercial fishery statistics employed in the analysis. Special thanks go to Kenneth N. Baxter for his painstaking computation of estimates of fishing effort.

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STUDY OF LOSS AND DELAY OF SALMON PASSING ROCK ISLAND DAM, COLUMBIA RIVER, 1954–56

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ABSTRACT

To determine loss or delay of salmonids in passing Rock Island Dam on the Columbia River, and whether such loss or delay was associated with the right bank ladder, salmon were tagged and released both above and below the dam in 1954–56. They were subsequently observed passing through the fishways and recovered at upstream points. Most tagged fish released below the left and right bank fishway returned over the left, corresponding closely with the choice of ladders made by the untagged populations. Point estimates of sockeye salmon losses ranged from 0 to 42 percent. Tagging results (one season only) on spring chinook salmon indicated a loss of fish released below the right bank ladder, but no loss when total tag returns from below and above dam releases were compared; data failed to show that the dam caused losses of summer chinook. Tagged salmon released below the dam were delayed 2 to 4 days. Altering the right bank fishway may cause more fish to use it, but there is no clear evidence that such alterations will reduce overall loss or delay.

Rock Island Dam, completed in 1934, was the first dam built on the Columbia River. It is about 450 miles above the river's mouth in central Washington (fig. 1). A fishway was built at each end of the dam to pass anadromous fish and in 1936 a third was added near the middle of the dam to pass salmon observed congregating there. These ladders were the pool type, 20 feet wide, with a gradient of 1 to 10.

The dam was modified during 1951–53 by installing regulating gates in the spillway channel increasing the forebay elevation approximately 12 feet (fig. 2). Six new generating units were added in the powerhouse (located on the left side of the dam). These modifications necessitated changing the fishways to meet the new forebay level, and fish attraction flow was increased at the lower end of the left (looking downstream) ladder to counteract the effect of increased flow from the turbine units. Although fishery agencies requested changes at the lower end of the right ladder to provide better entrance conditions and additional attraction flow, nothing was done at the time. The entrance of the right ladder at three different water levels is shown in figure 3.

The Federal Power Commission, in granting a license amendment for the modification of Rock Island Dam, reserved the right to require altering the lower end of the right ladder if substantial evidence were presented that such alterations or modifications were required for effective conservation of fish life resources of the Columbia River. Any such altering was to begin before Dec. 1, 1960.

The size of anadromous fish runs passing Rock Island is shown in table 1. Fewer of the fish have used the right ladder since the dam was modified. During the period 1936–52, for example, the counts of salmon and steelhead at the three ladders were distributed as follows: Left ladder, 47.8 percent; center ladder, 22.5 percent; right ladder, 29.7 percent. For the period 1953–56 (after modification of the dam), the counts were these: Left ladder, 73.7 percent;

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center ladder, 11.6 percent; and right ladder, 14.7 percent.

This report describes tagging details and the results of experiments at Rock Island Dam to determine whether the dam caused loss or delay to these runs, and whether loss or delay was associated with the failure of fish to find and use the dam's right bank fishway.

TABLE 1.—*Chinook and sockeye salmon and steelhead trout counted at Rock Island Dam, 1933–56* [1]

Year	Number of fish counted		
	Chinook	Sockeye	Steelhead trout
1933	5,668	40,737	1,055
1934	7,115	2,227	583
1935	16,305	14,013	5,418
1936	7,290	16,500	2,373
1937	5,133	15,089	2,214
1938	5,795	17,095	2,399
1939 [2]	11,206	19,591	5,425
1940	9,512	27,093	5,220
1941	2,507	963	3,513
1942	6,833	16,340	3,693
1943	11,129	17,522	2,315
1944	3,364	5,035	1,338
1945	5,699	7,148	1,118
1946	9,981	45,030	1,779
1947	11,717	79,831	1,971
1948	7,083	84,184	2,360
1949	12,353	18,600	2,470
1950	10,348	50,134	1,852
1951	18,752	101,826	3,121
1952	20,121	114,349	2,883
1953	31,080	151,747	4,001
1954	33,283	91,234	5,406
1955	25,658	155,055	3,141
1956	25,085	92,443	1,540

[1] Silver salmon (*O. kisutch*) averaged about 60 fish per year during this period.

[2] Grand Coulee Dam blocked upriver migration commencing this year.

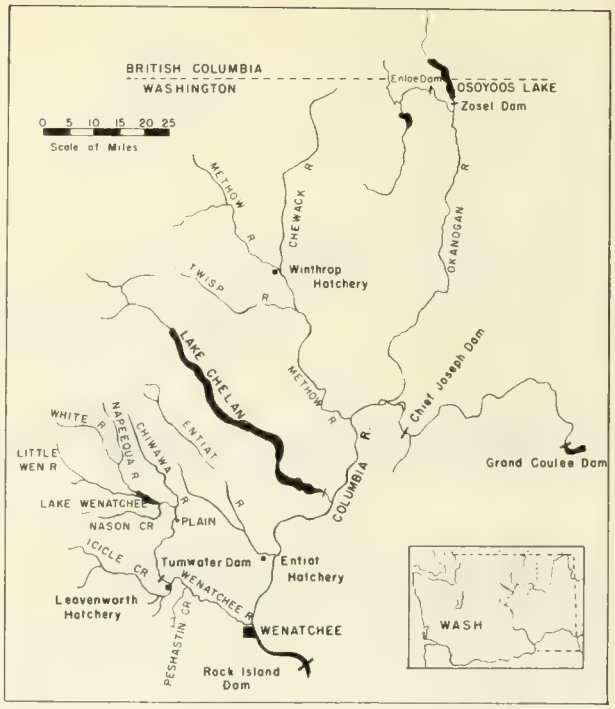

FIGURE 1.—Columbia River watershead between Rock Island and Grand Coulee Dams.

METHOD OF TAGGING

Preliminary experiments on tagging and methods of catching salmon were performed in 1953 followed by full-scale experiments in 1954 through 1956 on chinook (*Oncorhynchus tshawytscha*) and sockeye salmon (*O. nerka*). We planned to tag steelhead trout (*Salmo gairdneri*) but too few (17 to 32 each year) were captured and tagged for subsequent analysis.

Salmon were trapped at the upstream edge of the counting boards within the left and right fishways and at the upstream outlet of the left ladder. (Earlier attempts to catch quantities of fish for tagging below the dam were unsuccessful.) The trapped fish were transferred to tank trucks and hauled to the tagging sites located approximately 1,000 feet below the dam on each side of the river in 1954 and 1955. In 1956, tagged salmon were released off the downstream face of the dam close to the left or right ladder. The fish were lowered to water level in canvas bags filled with water (fig. 4). Forebay tag releases were from a trap located at the left ladder exit, and at sites on both sides of the river about 1 mile above the dam.

Various tag colors or shapes were used for the experiments at Rock Island Dam (fig. 5). Tags applied in the forebay differed from those used below the dam. Serially numbered plastic disks in combination with plastic bars formed one series of combinations, and serially numbered plastic disks with vinyl tubing and vinyl-coated nylon formed another series used below the dam. These were attached to each fish by nickel pins inserted through the body just below the dorsal fin. All tags were applied in pairs so that the same color or kind of tag showed on both sides of the fish. During 1954–55, the salmon were tagged while held in canvas-lined, cradle-type boxes. In 1956, the boxes were filled with water and the salmon were held under water during tagging.

Fish counters at the dam identified and recorded the tags as tagged fish crossed the counting boards. Display boards containing all tag samples were

FIGURE 2a.—Rock Island Dam before modification.

placed in the counting rooms for reference but counters were not told of the tag applied each day.

Upstream tag recoveries were made from spawning ground surveys, at fish hatcheries, and from fish counters' observations at Tumwater and Zosel Dams (fig. 1). As different colors and combinations of tags were used for each experiment, a tag observed on a live fish provided the same information as an actual recovery, except for the identity of the particular fish. Therefore, upstream tag recoveries include both visual observations of tags and actual recoveries.

To determine mortalities at the dam, we analyzed and compared the percentage tag returns at Rock Island from releases below the left and right bank ladders; for upstream tag returns we compared recovery ratios from the different release areas above and below the dam. In addition, percentage tag returns from the two release areas below the dam were compared by date of tagging and by volume of water flow at Rock Island. To determine delay we computed the elapsed day-out (number of days between tagging and subsequent tag observations) periods of tag returns at Rock Island; for upstream returns we computed the difference in day-out periods for releases above and below the dam.

ESTIMATION OF TOTAL UPSTREAM RECOVERIES OF TAGGED SOCKEYE

Upstream tag recoveries and observations for the 1954–56 individual sockeye experiments at Rock Island are given in table 2. The numbers of tagged fish released are given by date, location, and age group. Releases at the four locations in the vicinity of the dam were designated as follows: below dam, left bank; below dam, right bank; above dam, left bank; above dam, right bank. The two age groups represented in the releases of tagged fish were 3-year-old sockeye, recognized by their small size, and sockeye over 3 years old. Most of the fish in the latter group were 4 years old; hence, this group is designated as 4-year-old sockeye.

The recoveries from each release lot are given by area of recovery above the dam: (1) Tumwater

FIGURE 2b.—Rock Island Dam after modification.

Dam on the Wenatchee River; (2) Zosel Dam on the Okanogan River; (3) Okanogan River spawning grounds above Zosel Dam; and (4) all other areas combined.

In addition to the recovered tagged fish, numerous tagged sockeye were observed, but not recovered, in the recovery areas. These could be assigned to tagging date and release location, because different color combinations of tags were used for different release date-location combinations. They could not be individually assigned to age groups, however, hence, it is necessary to estimate the age composition of the tagged fish observed.

Spawning ground surveys of the Columbia River tributaries above Rock Island Dam indicated that 3-year-old sockeye migrate only to the Okanogan system, where they are found in varying numbers and proportions. On the basis of these surveys, together with the absence of recoveries of tagged 3-year-old sockeye in recovery areas 1 and 4, it is reasonable to assume that all the tagged fish observed in recovery areas 1 and 4 were 4-year-old sockeye.

The age composition of the tagged fish observed in recovery areas 2 and 3 can be estimated from proportions of 3-year-old sockeye in the recoveries from areas 2 and 3. Multiplying the proportions of 3-year-old sockeye in the recovery samples by the number of tagged fish observed provides estimates of the numbers of 3-year-old sockeye among the tagged fish observed. The numbers of 4-year-old sockeye among the tagged fish observed are obtained by subtraction. Table 3 shows the estimated numbers of 3- and 4-year-old sockeye observed in recovery areas 2 and 3.

In a number of instances, tagged sockeye recovered at Zosel Dam (recovery area 2) and released again after being checked for tag number and tag color were recovered a second time on the spawning grounds above Zosel Dam (recovery area 3). It is likely, therefore, that other tagged fish recovered or observed at Zosel Dam also were observed or recovered in recovery area 3. It is likely also that some tagged fish observed on the

spawning grounds subsequently were recovered. Such double recoveries or observations result in a tagged fish being counted two or more times in recovery areas 2 and 3.

To estimate the number of tagged individuals in the recovery-observations totals, we use the following expression:

$$S = R_2 + R_3 + O_2 + O_3 - R_{23} - \frac{R_{23}}{R_2}(O_2) - \left(\frac{O_3}{R_3}\right)\left(\frac{R_{23}}{R_2}\right)(R_2 + O_2)$$

Where, for each tag release group (age-release area-year combination),

R_2=number of tagged fish recovered at Zosel Dam
R_3=number of tagged fish recovered in area 3
O_2=number of tagged fish observed at Zosel Dam
O_3=number of tagged fish observed in area 3
R_{23}=number of tagged fish recovered at Zosel Dam and also in area 3

The first negative term corrects for double recoveries of tagged fish; the second negative term corrects for recoveries in area 3 of tagged fish observed at Zosel Dam; the last negative term corrects for observations in area 3 of tagged fish recovered or observed at Zosel Dam. The quantity, S, is referred to as the estimated total single recoveries.

Table 4 shows the recoveries, double recoveries, observations, estimated duplicate recovery-observations, and estimated total single recoveries for each release group.

TABLE 2.—*Sockeye salmon tagging data at Rock Island Dam*

[1954]

Area and date	Number released [1]	Number recovered								Number observed, age undetermined			
		3-year				4-year							
		Area of recovery				Area of recovery				Area where observed			
		1	2	3	4	1	2	3	4	1	2	3	4
Below dam, left bank:													
July 16	44 (2 42)	0	1	0	0	2	3	3	0	1	3	0	0
20	73 (7 66)	0	3	0	0	5	4	6	0	3	4	0	0
22	135 (27 108)	0	2	1	0	10	3	5	0	10	19	0	1
23	131 (21 110)	0	2	2	0	9	3	5	1	18	9	0	0
28	110 (20 90)	0	0	0	0	2	1	0	1	22	7	0	0
30	135 (62 73)	0	17	1	0	5	1	4	2	10	13	0	0
Aug. 6	125 (73 52)	0	6	2	0	3	0	0	1	6	16	1	0
11	31 (18 13)	0	0	0	0	2	0	0	0	1	0	2	0
13	18 (14 4)	0	1	0	0	0	0	0	1	0	2	0	0
Total	802 (244 558)	0	32	6	0	38	15	23	6	71	73	3	1
Below dam, right bank:													
July 1	1 (0 1)	0	0	0	0	0	0	0	0	0	0	0	0
7	7 (0 7)	0	0	0	0	1	0	0	0	0	0	0	1
8	14 (0 14)	0	0	0	0	0	0	0	0	1	0	1	0
21	126 (38 88)	0	2	0	0	2	3	2	1	7	23	1	0
22	25 (4 21)	0	0	0	0	1	0	0	1	2	2	1	0
27	83 (37 46)	0	2	1	0	0	0	1	1	10	18	0	0
29	63 (17 46)	9	4	1	0	3	1	0	1	6	9	0	0
Aug. 3	89 (43 46)	0	5	1	0	3	0	1	2	5	11	0	0
5	139 (82 57)	0	7	1	0	1	1	3	1	8	17	0	1
10	75 (43 32)	0	2	0	0	1	2	0	1	1	2	3	0
12	43 (25 18)	0	2	1	0	0	0	0	0	2	1	0	0
17	4 (1 3)	0	0	0	0	0	0	0	0	0	0	0	0
19	1 (0 1)	0	0	0	0	0	0	0	0	0	0	0	0
Total	670 (290 380)	0	24	5	0	12	7	7	8	42	83	6	2
Above dam, left bank:													
July 23	70 (14 56)	0	0	0	0	4	0	1	0	11	8	0	0
30	32 (8 24)	0	0	0	0	0	0	0	0	5	1	1	1
Aug. 4	30 (10 20)	0	0	1	0	1	0	0	0	7	4	0	0
6	13 (4 9)	0	0	0	0	0	0	0	0	1	0	0	0
13	8 (2 6)	0	0	0	0	0	0	0	1	0	0	2	0
20	2 (0 2)	0	0	0	0	0	0	0	0	0	0	0	0
27	2 (1 1)	0	0	0	0	0	0	0	0	0	0	0	0
Total	157 (39 118)	0	0	1	0	5	0	1	1	24	13	3	1
Summary:													
Below dam totals	1,472 (534 938)	0	56	11	0	50	22	30	14	113	156	9	3
Above dam totals [2]	157 (39 118)	0	0	1	0	5	0	1	1	24	13	3	1

See footnotes at end of table.

TABLE 2.—*Sockeye salmon tagging data at Rock Island Dam*—Continued

[1955]

Area and date	Number released [1]	Number recovered								Number observed, age undetermined			
		3-year				4-year							
		Area of recovery				Area of recovery				Area where observed			
		1	2	3	4	1	2	3	4	1	2	3	4
Below dam, left bank:													
July 21	59 (0 59)	0	0	0	0	9	2	8	0	1	0	2	0
26	111 (3 108)	0	0	1	0	14	2	9	1	3	0	1	1
28	95 (4 91)	0	0	0	0	24	1	5	0	2	0	1	1
29	92 (4 88)	0	0	0	0	20	3	4	1	1	0	1	0
Aug. 2	50 (3 47)	0	1	0	0	4	0	3	1	0	0	0	1
3	79 (3 76)	0	0	0	0	26	4	3	0	6	1	1	0
5	71 (11 60)	0	3	0	0	12	4	2	2	3	0	3	0
10	22 (4 18)	0	1	0	0	2	1	0	0	3	0	0	0
Total	579 (32 547)	0	5	1	0	111	17	34	5	19	1	9	3
Below dam, right bank:													
July 19	67 (1 66)	0	0	0	0	4	1	11	0	2	2	1	0
20	55 (2 53)	0	1	0	0	2	3	9	1	1	2	0	0
22	45 (4 41)	0	2	0	0	6	0	3	0	2	0	1	0
26	78 (5 73)	0	0	0	0	10	5	4	0	3	0	3	0
27	73 (3 70)	0	0	0	0	12	2	8	2	3	1	0	0
28	76 (5 71)	0	0	1	0	4	4	9	3	4	1	2	0
Aug. 2	24 (5 19)	0	0	0	0	4	1	1	0	1	0	1	0
4	101 (14 87)	0	1	0	0	16	5	1	1	1	0	2	0
9	41 (5 36)	0	0	0	0	6	1	2	0	2	0	0	1
11	37 (9 28)	0	1	0	0	5	0	0	0	3	0	0	0
Total	597 (53 544)	0	5	1	0	69	22	48	7	22	6	10	1
Above dam, left bank:													
July 21	61 (1 60)	0	0	0	0	8	4	8	1	7	0	0	0
29	60 (3 57)	0	0	0	0	5	2	5	0	2	0	2	0
Aug. 3	64 (1 63)	0	0	0	0	14	3	1	2	5	0	1	0
5	8 (1 7)	0	0	0	0	1	0	1	0	0	1	1	0
12	17 (5 12)	0	0	0	0	1	0	0	0	0	0	1	0
Total	210 (11 199)	0	0	0	0	29	9	15	3	14	1	5	0
Above dam, right bank:													
July 20	44 (1 43)	0	0	0	0	1	6	5	0	5	2	1	1
22	49 (2 47)	0	0	0	0	3	1	5	1	3	0	1	0
27	50 (3 47)	0	0	0	0	5	0	6	0	0	0	1	0
Total	143 (6 137)	0	0	0	0	9	7	16	1	8	2	3	1
Summary:													
Below dam total	1,176 (85 1,091)	0	10	2	0	180	39	82	12	41	7	19	4
Above dam total	353 (17 336)	0	0	0	0	38	16	31	4	22	3	8	1
[1956]													
Below dam, left bank:													
July 13	90 (1 89)	0	0	0	0	13	0	5	2	7	1	2	0
19	75 (15 60)	0	0	1	0	10	1	5	0	2	0	2	0
28	91 (38 53)	0	1	1	0	26	0	1	0	2	2	0	1
25	47 (9 38)	0	0	0	0	8	0	1	1	2	0	3	1
Aug. 1	41 (19 22)	0	0	1	0	4	1	1	0	0	2	0	0
3	49 (27 22)	0	2	0	0	2	0	0	1	3	2	4	0
Total	393 (109 284)	0	3	3	0	63	2	13	4	16	7	11	2
Below dam, right bank:													
July 10	24 (0 24)	0	0	0	0	2	0	0	1	1	0	3	0
12	20 (0 20)	0	0	0	0	0	0	0	0	0	0	5	0
17	80 (4 76)	0	0	0	0	10	0	5	0	2	1	9	0
24	75 (34 41)	0	2	2	0	15	0	2	0	1	0	1	0
26	96 (30 66)	0	0	0	0	27	0	2	0	2	0	1	0
31	33 (15 18)	0	0	1	0	4	0	0	0	1	1	2	0
Aug. 2	30 (24 6)	0	2	1	0	2	0	0	0	0	2	0	0
Total	358 (107 251)	0	4	4	0	60	0	9	1	7	4	21	0
Above dam, left bank:													
July 11	41 (0 41)	0	0	0	0	3	0	5	1	5	0	0	0
20	98 (21 77)	0	0	0	0	30	0	3	2	5	0	0	0
25	90 (36 54)	0	1	0	0	15	0	3	0	6	1	0	0
27	73 (26 47)	0	1	2	0	21	0	0	1	2	0	1	1
31	35 (19 16)	0	2	0	0	4	0	0	1	1	1	1	0
Aug. 1	19 (5 14)	0	0	1	0	5	0	0	0	0	0	0	0
2	46 (25 21)	0	1	1	0	4	0	0	0	0	1	1	1
Total	402 (132 270)	0	5	4	0	82	0	11	5	19	3	3	2
Above dam, right bank:													
July 18	19 (3 16)	0	0	0	0	3	0	1	0	0	0	0	0
Total	19 (3 16)	0	0	0	0	3	0	1	0	0	0	0	0
Summary:													
Below dam totals	751 (216 535)	0	7	7	0	123	2	22	5	23	11	32	2
Above dam totals	421 (135 286)	0	5	4	0	85	0	2	5	3	19	3	2

[1] Figures in parentheses represent the number of 3- and 4-year-old fish, respectively, making up the total.
[2] No tagged fish were released above dam, right bank, in 1954.

Table 5 contains a summary of releases of tagged sockeye by age group and release area and recoveries at Tumwater Dam, in the Okanogan River, and in other areas combined. The estimated total recoveries of 3- and 4-year-old tagged sockeye in the Okanogan system also are shown.

DETERMINATION OF MORTALITIES AT ROCK ISLAND

If there were a substantial loss of fish below Rock Island Dam, whether caused by a failure of fish to find a fish ladder or for other reasons, there should be a greater upstream recovery of fish tagged and released above the dam than of fish similarly tagged and released below the dam. Mortalities also should be reflected by the number of tagged fish passing the dam compared to the number released. We found, as shown later, that the fish counters' records of tagged fish passing Rock Island Dam from releases below the dam did not give completely reliable data on fish mortalities (assuming unaccounted-for tags as mortalities caused by the dam). Results of the upstream tag recovery comparisons are presented first, followed by the results obtained at Rock Island Dam.

RETURNS FROM UPSTREAM

Sockeye

Analysis of the tagging data to estimate mortalities is complicated by the presence of different races of sockeye in the tagging groups, by different age groups, and by the unequal effort expended recovering tags from different races and age groups. The sockeye run separates a short distance above Rock Island Dam, with some fish going into the Wenatchee River system and some fish up the Columbia River to the Okanogan River system. A few sockeye show up at the Entiat and Winthrop fish hatcheries and in Icicle Creek below the Leavenworth fish hatchery. As stated previously, 3-year-old sockeye are restricted to the Okanogan system and 4-year-old fish are found in all areas. We could effectively observe or recover all tagged fish passing Tumwater Dam on the Wenatchee River while on the way to spawning areas. In the Okanogan system, however, tag recoveries were made during stream surveys of the spawning areas and sampling at Zosel Dam on the Okanogan River, Thus, the recovery effort for tags on fish in the Wenatchee and Okanogan systems was not equal. Adding to these complications is the very probable loss of some tagged fish due to a tagging mortality or to straying.

Taking a simple approach, we have estimated the mortality rates from the ratios of the recovery proportions of tagged fish recovered from above- and below-dam releases. We made the following general assumptions: (1) The chance of recovering tagged fish is the same regardless of tagging date and tagging site, (2) racial proportions in the tagging lots are the same for the different areas of release, and (3) the chance of a tag recovery or observation is independent of tag type or color.

TABLE 3.—*Estimated numbers of 3- and 4-year-old tagged sockeye salmon in recovery areas 2 and 3, by year and release area*

Year and release area	Recovery Area 2										Recovery Area 3									
	Number recovered			Percent 3's	Number observed	Estimated numbers observed		Estimated totals			Number recovered			Percent 3's	Number observed	Estimated numbers observed		Estimated totals		
	3's	4's	Total			3's	4's	3's	4's	Totals	3's	4's	Total			3's	4's	3's	4's	Total
1954																				
Below dam, left bank	32	15	47	68	73	50	23	82	38	120	6	23	29	21	3	1	2	7	25	32
Below dam, right bank	24	7	31	77	83	64	19	88	26	114	5	7	12	42	6	2	4	7	11	18
Above dam, left bank	0	0	0	.....	13	~7	~6	7	6	13	1	1	2	50	3	1	2	2	3	5
1955																				
Below dam, left bank	5	17	22	23	1	0	1	5	18	23	1	34	35	3	9	0	9	1	43	44
Below dam, right bank	5	22	27	18	6	1	5	6	27	33	1	48	49	2	10	0	10	1	58	59
Above dam, left bank	0	9	9	0	1	0	1	0	10	10	0	15	15	0	5	0	5	0	20	20
Above dam, right bank	0	7	7	0	2	0	2	0	9	9	0	16	16	0	3	0	3	0	19	19
1956																				
Below dam, left bank	3	2	5	60	7	4	3	7	5	12	3	13	16	19	11	2	9	5	22	27
Below dam, right bank	4	0	4	100	4	4	0	8	0	8	4	9	13	31	21	6	15	10	24	34
Above dam, left bank	5	0	5	100	3	3	0	8	0	8	4	11	15	27	3	1	2	5	13	18
Above dam, right bank	0	0	0	.....	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	1

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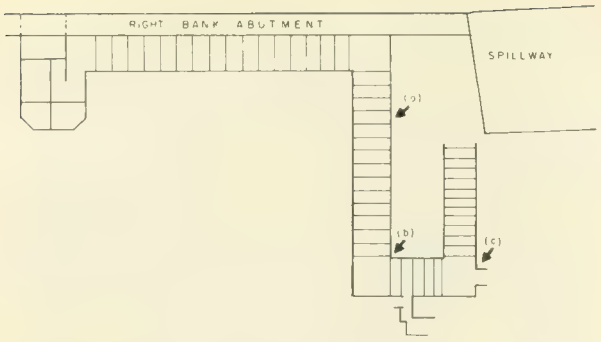


FIGURE 3.—Lower end of right ladder at different water levels. Diagrammatic sketch shows photo areas: (a) high flows; (b) intermediate flows; and (c) low flows.

The estimating equation for survival rate (k) is given by

$$\frac{R_b/T_b}{R_a/T_a}$$

where

T_b=Number of tagged fish released below dam

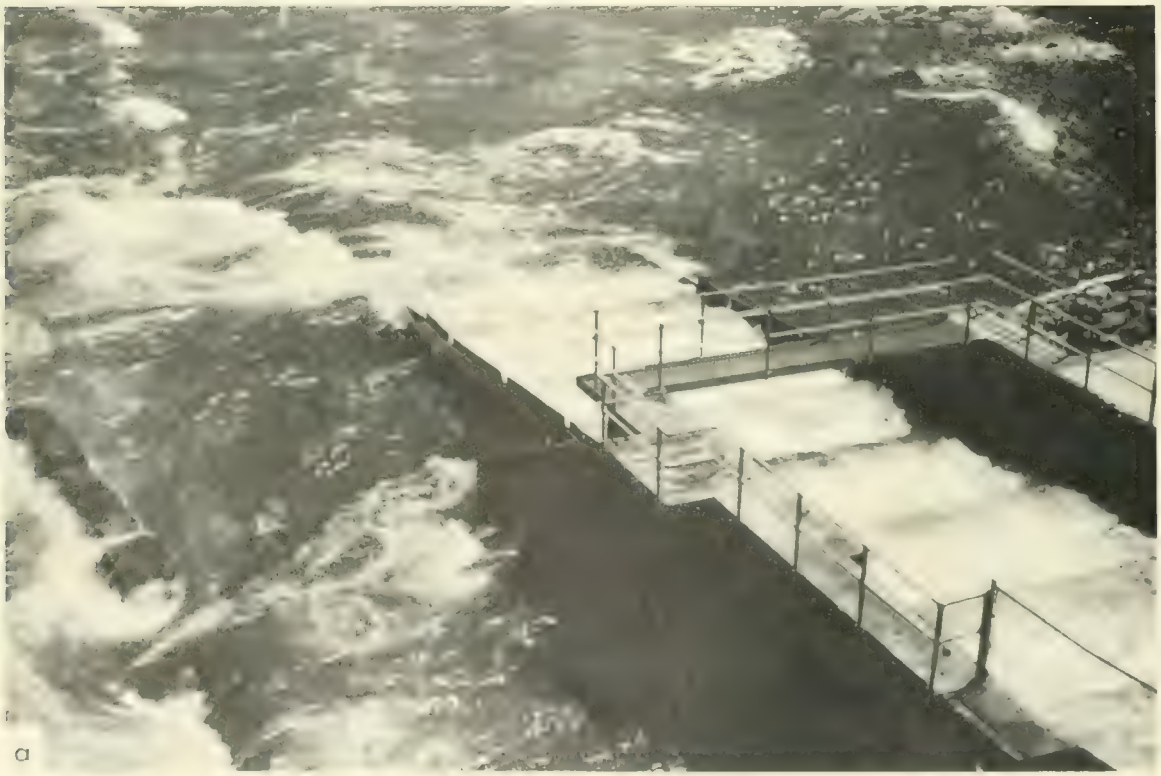
R_b=Number of tagged fish recovered from T_b

T_a=Number of tagged fish released above the dam

R_a=Number of tagged fish recovered from T_a

If the value of the ratio is one then mortality is zero. Where the value of this ratio is less than one, then the corresponding mortality rate is given by $1-k$.

The results of tagging experiments on the 3-year-old sockeye are shown in table 6. It is apparent that too few 3-year-old sockeye were tagged above the dam to afford meaningful comparisons between above and below dam experiments and to give estimates of mortality rates. No mortalities were evident from the limited data available. A comparison of the recovery proportions of tagged fish released below the left and right fishways shows right bank releases having a higher recovery rate in 2 of the 3 years. For all years combined the two recovery rates were nearly identical.



a

b

c

FIGURE 4.—Lowering tagged fish off the deck of the dam.

In table 7 are listed the estimates of mortalities based on all 4-year-old sockeye recoveries.

Compared with the proportions of tagged fish recovered from the area AL (left bank above the dam) releases, tagged fish released on the left bank below the dam suffered mortalities of about 10, 6, and 16 percent in 1954, 1955, and 1956, respectively. Tagged fish released on the right bank below the dam suffered mortalities of about 22, 12, and 18 percent in the corresponding years. We would conclude from these point estimates that tagged fish released below the dam suffered a mortality due to the dam, and that the mortality rate was greater for fish released on the right bank below the dam than for fish released on the left bank below the dam.

Compared with the proportions of tagged fish recovered from the AR (right bank above the dam) releases, tagged fish released on the left bank below the dam suffered no mortality due to the dam in either 1955 or 1956. Neither did tagged fish released on the right bank below the dam. The point estimates for 1956, it should be recognized, are based on a release of only 16 fish in area AR.

In combining the data for the 3 years, we could conclude, on the basis of recoveries from area AL releases, that tagged fish released on the left bank below the dam suffered a mortality of about 16 percent because of the dam, and that tagged fish released on the right bank below the dam suffered a mortality of about 21 percent because of the dam. Little or no mortality was indicated on the basis of releases in area AR (0 and 2 percent).

When comparing proportions of tagged fish recovered from total releases below the dam with all releases above the dam, we obtained point estimates of mortalities due to the dam of about 15 percent in 1954, 4 percent in 1955, 15 percent in 1956, and 15 percent for all years.

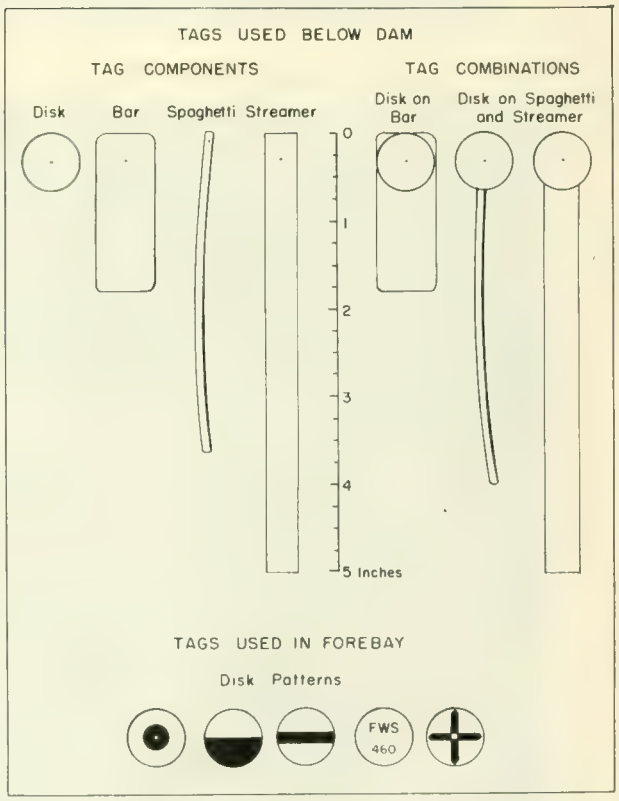


FIGURE 5.—Kinds of tags used during the Rock Island tagging experiments.

TABLE 4.—*Estimates of total single recoveries in the Okanogan system by age group and release area, Rock Island Dam sockeye tagging, 1954–56*

Year and release area	Number recovered area 2 (R_2)	Number recovered area 3 (R_3)	Number observed area 2 (O_2)	Number observed area 3 (O_3)	$R_2+R_3+O_2+O_3$	Number recovered second time in area 3 (R_{23})	$\frac{R_{23}}{R_2}(O_2)$	$\frac{O_3}{R_3}\left(\frac{R_{23}}{R_2}\right)(R_2+O_2)$	Total correction	Estimated total single recoveries (S)
	3-year-old sockeye									
1954										
Below dam, left bank	32	6	50	1	89	1	2	0	3	86
Below dam, right bank	24	5	64	2	95	0	0	0	0	95
Above dam, left bank	0	1	7	1	9	0	0	0	0	9
1955										
Below dam, left bank	5	1	0	0	6	0	0	0	0	6
Below dam, right bank	5	1	1	0	7	0	0	0	0	7
Above dam, left bank	0	0	0	0	0	0	0	0	0	0
Above dam, right bank	0	0	0	0	0	0	0	0	0	0
1956										
Below dam, left bank	3	3	4	2	12	0	0	0	0	12
Below dam, right bank	4	4	4	6	18	0	0	0	0	18
Above dam, left bank	5	4	3	1	13	0	0	0	0	13
Above dam, right bank	0	0	0	0	0	0	0	0	0	0
	4-year-old sockeye									
1954										
Below dam, left bank	15	23	23	2	63	3	5	1	9	54
Below dam, right bank	7	7	19	4	37	0	0	0	0	37
Above dam, left bank	0	1	6	2	9	0	0	0	0	9
1955										
Below dam, left bank	17	34	1	9	61	2	0	1	3	58
Below dam, right bank	22	48	5	10	85	1	0	0	1	84
Above dam, left bank	9	15	1	5	30	0	0	0	0	30
Above dam, right bank	7	16	2	3	28	1	0	0	1	27
1956										
Below dam, left bank	2	13	3	9	27	1	2	2	5	22
Below dam, right bank	0	9	0	15	24	0	0	0	0	24
Above dam, left bank	0	11	0	2	13	0	0	0	0	13
Above dam, right bank	0	1	0	0	1	0	0	0	0	1

We observe from the estimated confidence limits that the lower limits bracket zero in most instances and range to about 5 percent. The upper limits range from 20 to about 46 percent.

Another procedure was to estimate mortality rates based on recoveries of 4-year-old sockeye at Tumwater Dam (table 8). Compared with the proportions of tagged fish recovered from area AL (left bank above the dam) releases, tagged fish from left bank-below releases suffered mortalities of about 21, 0, and 26 percent, respectively, for 1954, 1955, and 1956. Tagged fish released on the right bank below the dam suffered mortalities of about 42, 23, and 29 percent, respectively, for the same 3 years.

Compared with the proportions of tagged fish recovered from the area AR releases (right bank above the dam), the tagged fish released at the right and left banks below the dam suffered no mortalities.

Combining the data for the 3 years, we observe on the basis of area AL releases that tagged fish released below the left fishway suffered a mortality of about 22 percent and that tagged fish released below the right bank fishway suffered a mortality of about 39 percent. No mortality was indicated on the basis of releases in area AR; however, comparatively few fish were released there.

Point estimates of mortality rates, obtained from comparisons of proportions of tagged fish recovered from total releases below the dam with all releases above the dam are about 29 percent in 1954, 0 percent in 1955, 25 percent in 1956, and 21 percent for all years.

Considering the confidence limits of these mortality rates based on Tumwater Dam recoveries, we observe the lower limits to bracket zero in two instances and range to 28 percent. The upper limits range from about 32 to 66 percent.

It is readily apparent that the analyses of the sockeye tagging data gave conflicting results of mortalities caused by the dam. On the one hand, many experiments indicated substantial mortalities, and mortalities apparently were greater for fish released below the right bank fishway. On

TABLE 5.—*Summary of Rock Island Dam sockeye tagging data by age group, 1954–56*

Year and release area	Total number released	3-year-old sockeye		4-year-old sockeye				Estimated total Okanogan recoveries
		Number released	Estimated number recovered in Okanogan	Number released	Number recovered			
					Tumwater	Estimated in Okanogan	Other areas	
1954								
Below dam, left bank	802	244	86	558	109	54	7	140
Below dam, right bank	670	290	95	380	54	37	10	132
Total	1,472	534	181	938	163	91	17	272
Above dam, left bank	157	39	9	118	29	9	2	18
Total	157	39	9	118	29	9	2	18
1955								
Below dam, left bank	579	32	6	547	130	58	8	64
Below dam, right bank	597	53	7	544	91	84	8	91
Total	1,176	85	13	1,091	221	142	16	155
Above dam, left bank	210	11	0	199	43	30	3	30
Above dam, right bank	143	6	0	137	17	27	2	27
Total	353	17	0	336	60	57	5	57
1956								
Below dam, left bank	393	109	12	284	79	22	6	34
Below dam, right bank	358	107	18	251	67	24	1	42
Total	751	216	30	535	146	46	7	76
Above dam, left bank	402	132	13	270	101	13	7	26
Above dam, right bank	19	3	0	16	3	1	0	1
Total	421	135	13	286	104	14	7	27
Totals 1954–55–56								
Below dam, left bank	1,774	385	104	1,389	318	134	21	238
Below dam, right bank	1,625	450	120	1,175	212	145	19	265
Total	3,399	835	224	2,564	530	279	40	503
Above dam, left bank	769	182	22	587	173	52	12	74
Above dam, right bank	162	9	0	153	20	28	2	28
Total	931	191	22	740	193	80	14	102

the other hand, many of the experiments indicated no mortalities caused by the dam.

Returns from below the dam by date of tagging.—The upstream recoveries of tagged sockeye, released below the dam, indicated a fairly uniform pattern of returns for all experiments (figs. 6,7, and 8). As tagging experiments were alternated between left and right banks on alternate days, these graphs show a fairly consistent pattern of returns for both release areas and for the duration of the tagging season. The percent-recovered curve in 1954 assumed the shape of the numbers-tagged curve, with fewer returns from the tails of the experiments. Percentage returns for 1955 and 1956 show a remarkably uniform pattern. The large numbers tagged, shown for July 26 and 28 in 1955 and for July 24 in 1956, are the result of combining left and right bank experiments, as experiments were conducted on both banks on those dates. Returns of nearly 50 percent from the August 3, 1955, experiment (fig. 7) are a result of observing a large number of that day's tagged fish passing Tumwater Dam, more fish observed than for any other single experiment. It might be that this particular sample contained relatively more Wenatchee fish than the other samples.

Returns from below dam compared with water flow.—In order to determine the influence of different water levels on fish passage at Rock Island Dam, tag recoveries from releases at each bank below the dam were compared with water flow (figs. 9, 10, and 11). In general, the tag returns from both banks showed a fairly consistent pattern despite large changes in flow during the experiments.

The returns for 1954 merit attention, since fewer returns are indicated for experiments on August 10–13 during the low river flows (fig. 9). These

TABLE 6.—*Estimated mortality rates due to Rock Island Dam based on 3-year-old sockeye tag recoveries*

Year and release area	Number released	Estimate number recovered	Proportion recovered r_i	Estimate of mortality rates				
				$1-\frac{r_{BL}}{r_{AL}}$	$1-\frac{r_{BL}}{r_{AR}}$	$1-\frac{r_{BR}}{r_{AL}}$	$1-\frac{r_{BR}}{r_{AR}}$	$1-\frac{r_{BL}+r_{BR}}{r_{AL}+r_{AR}}$
1954								
Below dam, left bank	244	86	0.352	−0.524				
Below dam, right bank	290	95	.328			−0.420		
Total	534	181	.339					−0.468
Above dam, left bank	39	9	.231					
Total	39	9	.231					
1955								
Below dam, left bank	32	6	.188					
Below dam, right bank	53	7	.132					
Total	85	13	.153					
Above dam, left bank	11	0	0					
Above dam, right bank	6	0	0					
Total	17	0	0					
1956								
Below dam, left bank	109	12	.110	−.122				
Below dam, right bank	107	18	.168			−.714		
Total	216	30	.139					−.448
Above dam, left bank	132	13	.098					
Above dam, right bank	3	0	0					
Total	135	13	.096					
Totals *1954–55–56*								
Below dam, left bank	385	104	.270	−1.231				
Below dam, right bank	450	120	.267			−1.207		
Total	835	224	.268					−1.330
Above dam, left bank	182	22	.121					
Above dam, right bank	9	0	0					
Total	191	22	.115					

fewer returns undoubtedly are related to a diminished effort to recover tags from these experiments. Fish counting and tag observing were discontinued at Zosel Dam from August 20 to August 26, at a time when tagged fish were still passing and when the number of tags from the August 10–13 experiments should have peaked there. Therefore, with comparable recovery effort, tag returns from these experiments probably would have been greater than indicated. It is noted that the 1955 returns from this same time period, August 9–11, and for comparable water flows (fig. 10), were consistent with returns from earlier experiments occurring at high flows. It is evident, as shown by upstream tag returns, that changes in flows at Rock Island Dam had little effect on the ability of sockeye to pass the dam.

Chinook

In order to compare recovery ratios of chinook salmon tagged above and below the dam, it was necessary to separate the chinooks by race. Races at Rock Island Dam were reported by Fish and Hanavan (1948) as spring and summer chinook. Spring chinook, passing Rock Island Dam earlier in the season than summer chinook, migrated to smaller, more remote spawning streams. In these streams, tagged fish were much easier to observe and recover than in larger streams, such as the Wenatchee and lower Methow Rivers (the summer chinook spawning areas). Thus, recoveries from spring chinook tagging experiments were much greater than from experiments on summer chinook.

Upstream tag recoveries for all chinook experiments are given in table 9. Many samples were too small to compare returns statistically. Only in 1956 were sufficient fish obtained to release at the two banks below the dam and above the dam. Returns of spring chinooks tagged below the dam were virtually the same (27 percent) for the 3

TABLE 7.—*Estimated mortality rates due to Rock Island Dam based on total 4-year-old sockeye recoveries*

[95 percent confidence limits]

Year and release area	Number released	Estimate number recovered	Proportion recovered r_i	Estimates of mortality rates				
				$1-\frac{r_{BL}}{r_{AL}}$	$1-\frac{r_{BL}}{r_{AR}}$	$1-\frac{r_{BR}}{r_{AL}}$	$1-\frac{r_{BR}}{r_{AR}}$	$1-\frac{r_{BL}+r_{BR}}{r_{AL}+r_{AR}}$
1954								
Below dam, left bank	558	170	0.305	0.100 (−0.159 to 0.359).				
Below dam, right bank	380	101	.266			0.215 (−0.028 to 0.458).		
Total	938	271	.289					0.147 (−0.089 to 0.383).
Above dam, left bank	118	40	.339					
Total	118	40	.339					
1955								
Below dam, left bank	547	196	.358	0.064 (−0.136 to 0.264).	−0.065			
Below dam, right bank	544	183	.336			0.120 (−0.071 to 0.311).		
Total	1,091	379	.347					0.044 (−0.116 to 0.204).
Above dam, left bank	199	76	.382					
Above dam, right bank	137	46	.336					
Total	336	122	.363					
1956								
Below dam, left bank	284	107	.377	0.158 (−0.014 to 0.330).	−.508			
Below dam, right bank	251	92	.366			0.183 (0.008 to 0.358).	−0.464	
Total	535	199	.372					0.149 (0 to 0.298).
Above dam, left bank	270	121	.448					
Above dam, right bank	16	4	.250					
Total	286	125	.437					
Totals *1954–55–56*								
Below dam, left bank	1,389	473	.340	0.158 (0.053 to 0.263).	−.040			
Below dam, right bank	1,175	376	.320			0.208 (0.103 to 0.313).	0.022 (−0.221 to 0.265).	
Total	2,564	849	.331					0.147 (0.054 to 0.240).
Above dam, left bank	587	237	.404					
Above dam, right bank	153	50	.327					
Total	740	287	.388					

years. In 1956, returns from tagging at the right bank were considerably lower than those from the left bank; however, the reverse was true for 1955. No reasonable explanation can be offered for these differences. Perhaps conditions which may have caused low recoveries from the right bank one season were not present the other season, or it may have been chance that upstream recoveries varied as they did in the 2 years.

The data for 1956 indicated a loss of fish released below the right bank fishway when recovery proportions were compared to recovery proportions of fish released above the dam (19.5 percent compared to 24.4 percent). In terms of mortality rates, in the same manner as was done for the sockeye, this would indicate a 20 percent mortality for fish tagged below the right bank. No mortalities were indicated when comparing total returns from below the dam with returns from above the dam.

While summer chinook tag returns are comparatively few, the recovery ratios are consistent over the years and for the different areas of release. Only in 1954 was there an indication of mortalities for right bank tag releases (7.1 percent recovered compared with 7.8 percent recovered from above the dam). In the other 2 years there was no indication of mortalities. There was no indication

TABLE 8.—*Estimated mortality rates due to Rock Island Dam based on Wenatchee sockeye recoveries*

[95 Percent confidence limits]

Year and release area	Number released	Estimate number recovered	Proportion recovered r_1	Estimates of mortality rates and confidence limits				
				$1-\frac{r_{BL}}{r_{AL}}$	$1-\frac{r_{BL}}{r_{AR}}$	$1-\frac{r_{BR}}{r_{AL}}$	$1-\frac{r_{BR}}{r_{AR}}$	$1-\frac{r_{BL}+r_{BR}}{r_{AL}+r_{AR}}$
1954								
Below dam, left bank	558	109	0.195	0.207 (0.08 to 0.497).				
Below dam, right bank	380	54	.142			0.423 (0.186 to 0.660).		
Total	938	163	.174					0.293 (0.044 to 0.542).
Above dam, left bank	118	29	.246					
Total	118	29	.246					
1955								
Below dam, left bank	547	130	.238	−0.102	−0.919			
Below dam, right bank	544	91	.167			0.227 (−0.030 to 0.484).	−0.347	
Total	1,091	221	.203					−0.134.
Above dam, left bank	199	43	.216,					
Above dam, right bank	137	17	.124,					
Total	336	60	.179					
1956								
Below dam, left bank	284	79	.278	0.257 (0.072 to 0.442).	−.479			
Below dam, right bank	251	67	.267			0.286 (0.099 to 0.473).	−.420	
Total	535	146	.273					0.250 (0.089 to 0.411).
Above dam, left bank	270	101	.374					
Above dam, right bank	16	3	.188					
Total	286	104	.364					
Total, *1954–55–56*								
Below dam, left bank	1,389	318	.229	0.224 (0.099 to 0.349).	−.748			
Below dam, right bank	1,175	212	.180			0.390 (0.280 to 0.500).	−.374	
Total	2,564	530	.207					0.207 (0.092 to 0.322).
Above dam, left bank	587	173	.295					
Above dam, right bank	153	20	.131					
Total	740	193	.261					

TABLE 9.—*Upstream returns of tagged spring and summer chinook by area of released at Rock Island Dam, 1954–56*

Year and release area	Spring chinook			Summer chinook		
	Tagged	Recovered		Tagged	Recovered	
	Number	*Number*	*Percent*	*Number*	*Number*	*Percent*
1954						
Below dam, right bank	150	40	26.7	113	8	7.1
Below dam, left bank				80	7	8.8
Total below dam	150	40	26.7	193	15	7.8
Above dam				217	17	7.8
1955						
Below dam, right bank	122	38	31.1	66	10	15.2
Below dam, left bank	70	13	18.6	34	2	5.9
Total below dam	192	51	26.6	100	12	12.0
Above dam	3	1	33.3	99	9	9.1
1956						
Off dam, right side	159	31	19.5	92	11	12.0
Off dam, left side	154	53	34.4	113	11	9.7
Total off dam	313	84	26.8	205	22	10.7
Above dam	168	41	24.4	199	21	10.6

of mortalities when comparing total returns from above and below the dam.

In view of these similar recoveries of tagged chinook salmon released above and below Rock Island Dam, we cannot conclude that there is a substantial mortality caused by the dam. For spring chinooks, there are indications of a loss of fish released below the right bank ladder in 1956. Data are not available for determining if this loss exists for the other 2 years.

RETURNS AT ROCK ISLAND

Identity of Tags and Species

The correct identity of tag returns at Rock Island Dam depended upon the fish counters'

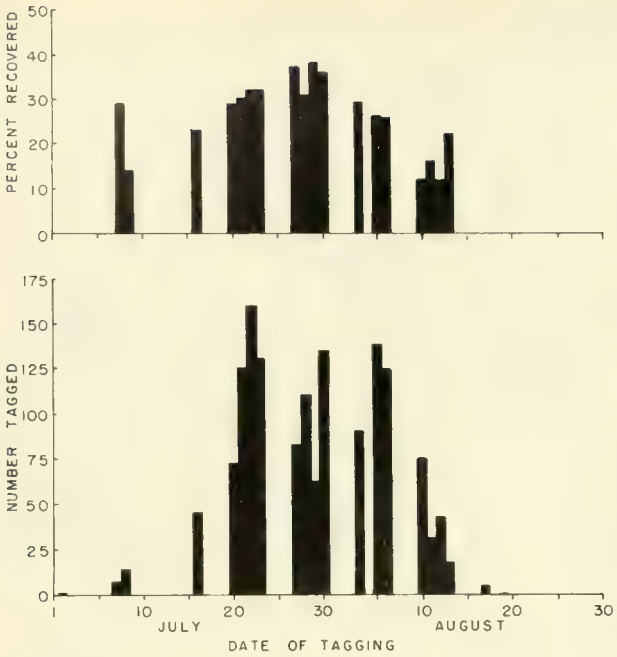


FIGURE 6.—Numbers of sockeye tagged below Rock Island Dam, and recoveries of tagged fish upstream, expressed as percentages of the number tagged each day, 1954.

identifying accurately the various tags and species of fish as the fish crossed counting boards. The tags were more difficult to identify at Rock Island than at upstream points because of the need for counting large numbers of fish while simultaneously identifying tags, and because of the speed the fish moved across the counting boards. The misidentification of both tags and species was a source of error in the Rock Island tag return data as exemplified in the following illustrations:

1. In some of the 1954 experiments, fish counters recorded as tagged species which had not been tagged. In other experiments, they recorded greater numbers of tag observations of species than fish tagged, and on several occasions they counted fewer jack chinook in the traps than were tallied during subsequent tagging. We revised our tagging procedure for some experiments in 1954 to determine the magnitude of error in species identification. Instead of tagging all species with one color combination as was usually done, we tagged the various species with different color combinations and noted the returns as identified by the counters (table 10). Many chinooks (obviously jacks) were called sockeye. Jacks are precocious male chinooks, and are similar in size to sockeye. The error in mistaking sockeye for chinooks was relatively small. No tagged steelhead were reported by the counters at Rock Island Dam; one tagged steelhead, however, was observed upstream at Tumwater Dam. Similar errors were made in 1955 and 1956, although the fish counters were asked to keep the counting boards at the minimum depth consistent with efficient fish passage. The magnitude of error was not determined for these years.

2. The disproportionate returns of the different types of tags used gave evidence of errors in tag identity at Rock Island Dam. A far greater percentage of bar tags was observed at Rock Island in 1954 and 1955 than of spaghetti tags (table 11). Upstream, however, the percentage returns of the two tags were approximately the same for both years. The streamer tag was substituted

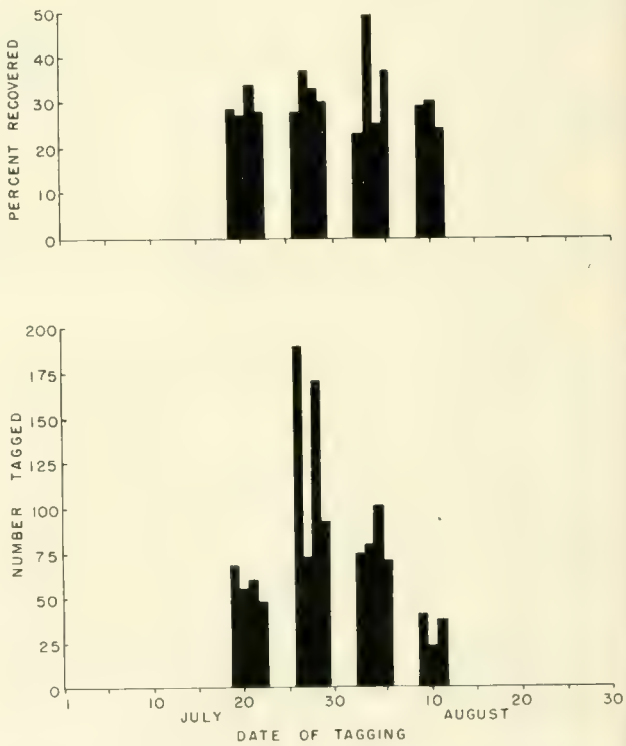


FIGURE 7.—Numbers of sockeye tagged below Rock Island Dam, and recoveries of tagged fish upstream, expressed as percentages of the number tagged each day, 1955.

for the spaghetti tag in 1956, and, as observed, returns were similar at Rock Island Dam and upstream for the two tags. It is evident, therefore, that the counters at Rock Island Dam did not discriminate between the tags in 1954 and 1955.

These errors in species and tag identification thus affected the reliability of the tag return data at Rock Island Dam, and the data must be used with caution.

TABLE 10.—*Errors in species identification at Rock Island Dam in 1954*

Species and date tagged	Tagged	Species reported by counters	Error
Chinook:	*Number*	*Number*	*Percent*
Aug. 5 [1]	6	0	
6	11	2 chinook, 4 sockeye	66.7
10	20 chinook, 2 steelhead	4 chinook, 9 sockeye	69.2
11	13 chinook, 2 steelhead	2 chinook, 10 sockeye	83.4
Total	50 chinook, 4 steelhead	10 chinook, 24 sockeye	70.5
Sockeye:			
Aug. 5	139	136 sockeye, 1 chinook	0.7
6	125	90 sockeye	0
10	75	71 sockeye [2], 8 chinook	10.1
11	31	22 sockeye, 2 chinook	8.3
Total	370	319 sockeye, 11 chinook	3.3

[1] The color and tag combination used here was also used 15 days previous. Some returns may have been attributed to the previous experiment.
[2] The total of 79 fish observed is an obvious error in tag identity.

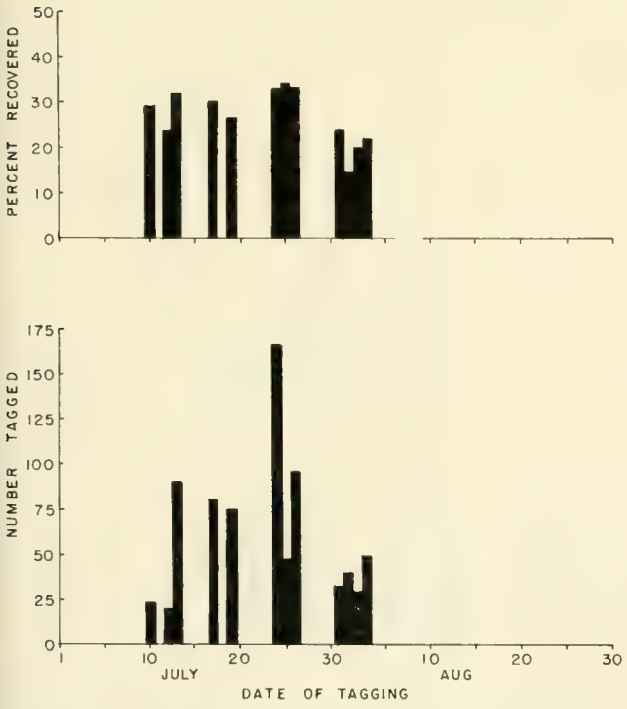


FIGURE 8.—Numbers of sockeye tagged below Rock Island Dam, and recoveries of tagged fish upstream, expressed as percentages of the number tagged each day, 1956.

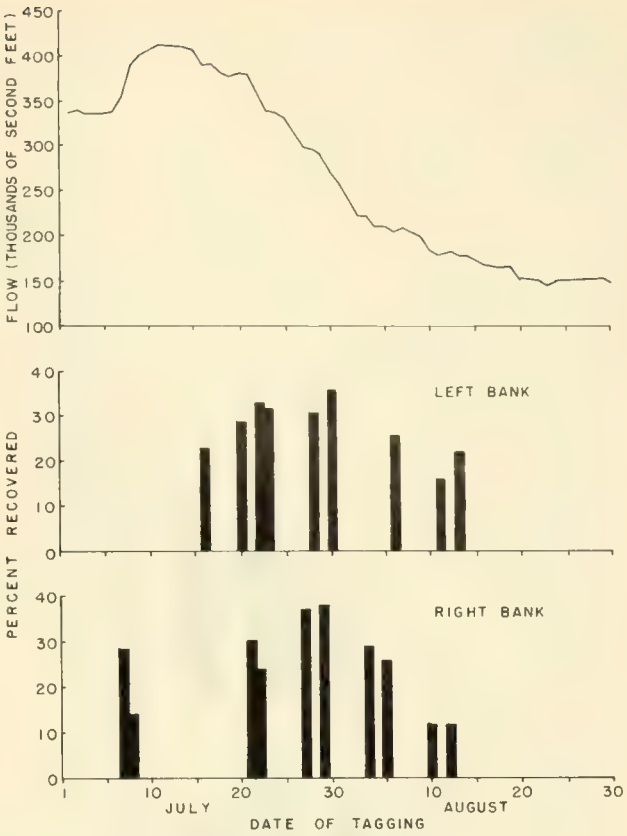


FIGURE 9.—Recoveries of tagged sockeye upstream expressed as percentages of the number tagged at each bank below, compared with water flow, 1954.

Sockeye and Chinook

The results of the fish counters' observations of tagged fish (including the few steelhead tagged) crossing the counting boards for the four seasons of tagging are shown in table 12. Although the salmon were released below the dam at various places on both sides of the river, most of the tags were observed at the left ladder. Comparatively few were recorded at the right ladder, even though roughly half of the salmon were released a short distance away. The counters observed 85 percent

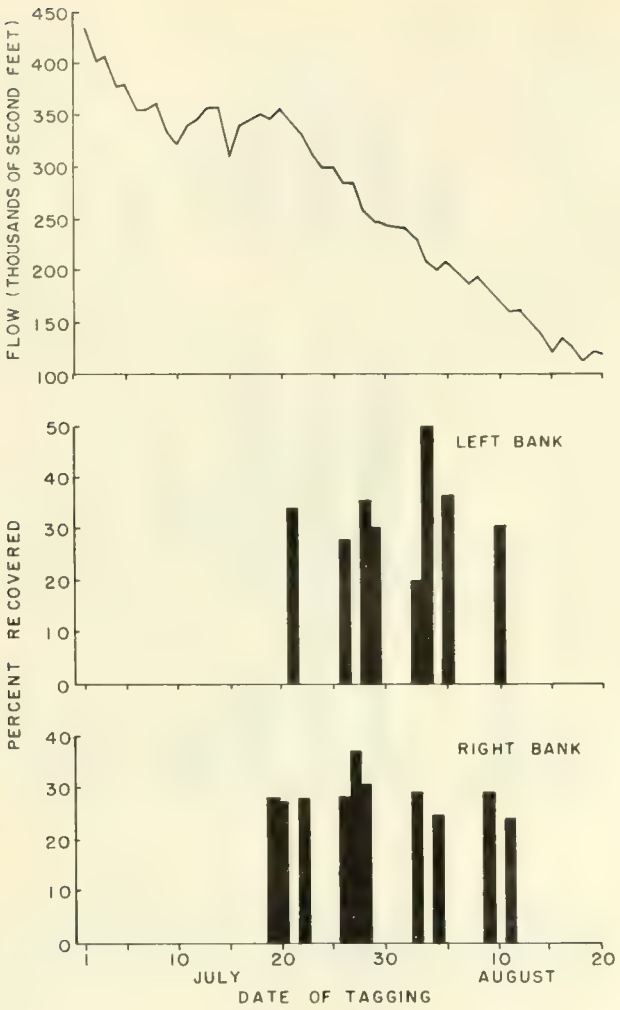


FIGURE 10.—Recoveries of tagged sockeye upstream expressed as percentages of the number tagged at each bank below, compared with water flow, 1955.

TABLE 11.—*Returns at Rock Island Dam and upstream of different kinds of tags used*

Year and kind of tag	Tagged	Returns at Rock Island		Tagged[2]	Returns upstream	
		Observed[1]			Recovered	
1954	*Number*	*Number*	*Percent*	*Number*	*Number*	*Percent*
Bar	1,284	1,121	87.3	1,260	320	25.4
Spaghetti	565	241	42.7	556	155	27.9
1955[3]						
Bar	1,174	855	72.8	1,000	317	31.7
Spaghetti	310	123	39.7	179	50	27.9
1956						
Bar	770	671	87.1	764	197	25.8
Streamer	509	423	83.1	506	128	25.3

[1] Undetermined tag observations at Rock Island not identified as bar, spaghetti, or streamer are omitted.

[2] Steelhead and those tagged fish removed at Rock Island for other experiments were omitted from this column.

[3] Only sockeye are included in the upstream returns in 1955 because of the unequal recovery effort spent on chinooks tagged with the two kinds of tags.

of the tags at the left and center ladders for the 4 years. While only 64 to 86 percent of the fish released below the dam were observed at the counting boards, we cannot say with certainty that these missing tags indicated mortalities caused by the dam.

These are some possible reasons for the apparent tag losses:

1. Counters did not identify tagged fish crossing the counting boards.
2. Tagging harmed the fish.
3. Fish lost the tags.
4. Tagged fish refused to re-pass the dam.
5. The dam itself caused mortalities.

The counters did overlook tagged salmon. On a few occasions when the forebay trap was fished, we captured tagged fish the counters had not reported. In some experiments, we recovered more tags upstream than the counters reported at

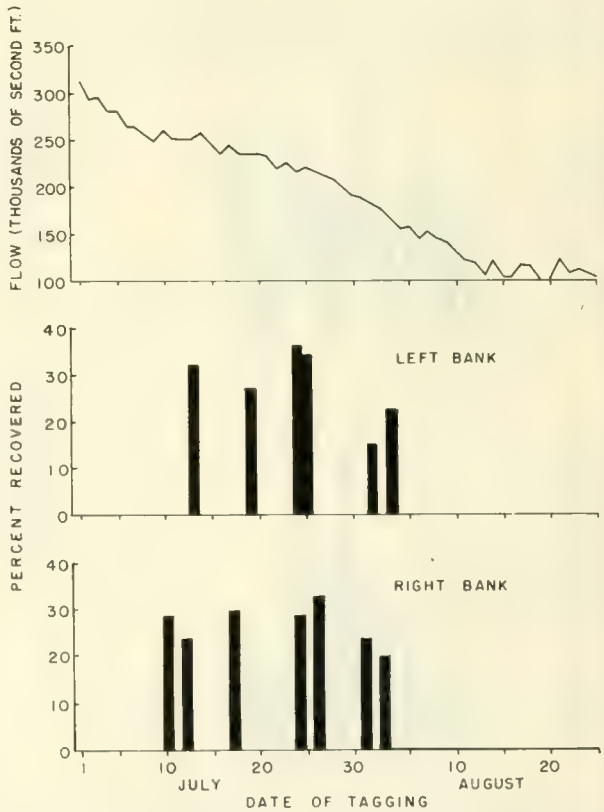


FIGURE 11.—Recoveries of tagged sockeye upstream expressed as percentages of the number tagged at each bank below, compared with water flow, 1956.

TABLE 12.—*Returns of tagged fish at Rock Island Dam by ladder, 1953–56*

Year	Tagged below Rock Island [1]	Observations by ladder						Total tag observations	
		Left		Center		Right			
	Number	*Number*	*Percent*	*Number*	*Percent*	*Number*	*Percent*	*Number*	*Percent*
1953	764	298	39.0	87	11.4	106	13.9	491	64.3
1954	1,849	788	42.6	399	21.6	188	10.2	1,375	74.4
1955	1,484	656	44.2	205	13.8	127	8.6	988	66.6
1956	1,279	724	56.6	214	16.7	156	12.2	1,094	85.5
Total	5,376	2,466	45.9	905	16.8	577	10.7	3,948	73.4

[1] Tagged members included chinook, sockeye, and steelhead.

Rock Island Dam. An illustration was the Bonneville experiment (app. p. 366) where a distinctive copper and black disk tag was used; only 6 of these tags were reported at Rock Island, but 14 were recovered upstream. In view of these examples, it was undoubtedly true that the counters missed tagged fish.

Tagging operations have caused mortalities. Schaefer (1951) concluded that there was a serious differential mortality among the tagged and untagged fish during the long migration between the Harrison trap and the Birkenhead River. Nelson[1] found a differential mortality between tagged and untagged sockeye migrating between Karluk River weir and weirs on the tributary spawning streams of Karluk Lake.

The loss of tags from tagged fish apparently was not a reason for the missing tags at Rock Island Dam. No tag-scarred salmon were reported by the counters at Rock Island Dam, and neither were any caught in the traps, though many tagged fish were captured there.

Tagged salmon may have refused to reenter the fishways after tagging. In 1956, five tagged salmon were observed in the Oregon Fish Commission's trap at McNary Dam, located approximately 160 river-miles downstream from Rock Island Dam. Also, a tagged sockeye was observed at the Redfish Lake weir in Idaho, about 700 river-miles from Rock Island Dam. Howard (1948) reported that handling during tagging operations at Cultus Lake, British Columbia, apparently caused some of the tagged sockeye to remain in the area immediately above the tagging location, rather than continue their migration. Undoubtedly some of the missing tags at Rock Island Dam could be attributed to straying.

Finally, mortalities could be caused by the dam. Mortalities were indicated for some experiments but not for others when comparing upstream recovery ratios from tagged fish released above and below the dam.

Returns by area of release.—The results of tag returns by ladder are shown in table 13. These data show a consistent pattern of passage over the ladders for the 3 years and for the two release areas. Only 6 to 12 percent of the fish used the right ladder.

The observed differences in returns from the two banks over the 3 years would indicate that right bank tag releases were not as successful in passing the dam as left bank releases.

TABLE 13.—*Tag returns by area of release and ladder, 1954–56*

Year and release area	Tagged	Observations by ladder [1]							
		Left		Center		Right		All ladders	
	Number	*Number*	*Percent*	*Number*	*Percent*	*Number*	*Percent*	*Number*	*Percent*
1954									
Right bank	950	389	40.9	192	20.2	80	8.4	661	69.6
Left bank	899	352	39.2	187	20.8	92	10.2	631	70.2
1955									
Right bank	793	311	39.2	91	11.5	47	5.9	449	56.6
Left bank	691	302	43.7	104	15.1	70	10.1	476	68.9
1956									
Right bank	616	331	53.7	94	15.3	76	12.3	501	81.3
Left bank	663	385	58.1	119	17.9	77	11.6	581	87.6

[1] Unidentifiable tags were excluded.

Since almost all of the fish were trapped in the left ladder or in the forebay trap at the head of this ladder, and since they were released at both banks below the dam, it was important to know whether these fish had learned the route for their second passage of the dam. Accordingly, the tag returns were listed by trapping site and by area of release (table 14). Regardless of where the fish were trapped or released, they returned in approximately the same ratio over the three ladders with the least returns always at the right ladder. It is evident that the salmon did not learn a route and then repeat this route for a second passage over the dam. Neither were they necessarily frightened away from a ladder, since the majority of fish returned to the left ladder, where most were trapped previously.

[1] Nelson, Philip R., unpublished data 1947 and 1948. U.S. Fish and Wildlife Service, Seattle, Wash.

TABLE 14.—*Tag returns by ladder of salmon trapped at both ladders and released at both banks below Rock Island Dam, 1954–55*

Year and trapping area	Area released	Tagged	Observations by ladder [1]					
			Left		Center		Right	
1954		*Number*	*Number*	*Percent*	*Number*	*Percent*	*Number*	*Percent*
Right ladder	Right bank	178	56	64.4	20	23.0	11	12.6
Left ladder	Right bank	748	331	57.9	172	30.1	69	12.1
Left ladder	Left bank	923	354	55.9	187	29.5	92	14.5
1955								
Right ladder	Right bank	363	169	72.5	49	21.0	15	6.4
Left ladder	Right bank	430	142	65.7	42	19.4	32	14.8
Left ladder	Left bank	691	302	63.4	104	21.8	70	14.7

[1] The percentage by ladder is based on total observations.

Tagged and untagged fish movements.—Table 15 shows the comparison of choice of ladders between tagged and untagged salmon for each season of tagging. Chinooks and sockeye were combined because of the error of confusing chinooks (jacks) with the sockeye. The percentage returns at the right ladder agreed closely with those of the untagged run. A somewhat larger proportion of the untagged run, compared with the tagged fish, chose the left ladder for passage. The percentage returns at the middle ladder were greater than the proportion of untagged fish at this ladder. This may be because right bank releases, failing to enter the right ladder, were attracted by the center ladder before the left ladder. Generally speaking, however, the tagged and untagged salmon were similar in their patterns of passage.

During the years of the tagging experiments, the four spillway regulating gates nearest the right ladder were kept closed so the high-velocity flows would not interfere with fish approaching along the right bank. In 1957, in order to test their influence on fish passage, these gates (one or more) were opened when most of the fish passed the dam. The percentage of chinooks and sockeye using this ladder in 1957 increased to 24 percent, compared to an average of 15 percent for 1953–56. This was the pattern of fish passage at the right ladder by species—chinooks, 19.8 percent; sockeye, 26.8 percent; and steelhead, 16.6 percent. No tagging was done in 1957, and a comparison of tagged fish movements could not be made. Apparently the salmons' choice of ladders can be influenced by manipulating the regulating gates and by the resulting changes in flow patterns below the dam.

TABLE 15.—Combined chinook and sockeye counts of the tag returns and the untagged runs by ladder, 1954–56

Year	Combined chinook and sockeye counts						Total
	Left ladder		Center ladder		Right ladder		
1954	*Number*	*Percent*	*Number*	*Percent*	*Number*	*Percent*	*Number*
Tagged	787	57.3	399	29.0	188	13.7	1,374
Untagged	86,439	70.0	17,144	13.9	19,892	16.1	123,475
1955							
Tagged	654	66.3	205	20.8	127	12.9	985
Untagged	139,555	77.4	22,415	12.4	18,448	10.2	180,418
1956							
Tagged	724	66.2	214	19.6	156	14.2	1,094
Untagged	88,154	75.0	18,697	15.9	10,677	9.1	117,528
Total 1954–1956.							
Tagged	2,165	62.7	818	22.7	471	13.6	3,454
Untagged	314,148	74.5	58,256	13.8	49,017	11.6	421,421

DETERMINATION OF DELAY AT ROCK ISLAND

In this paper delay means the period of time that Rock Island Dam checks the migration of salmon under present conditions.[2] Delay may cause salmon mortalities prior to spawning. Some causes of delay may be flood waters in rivers, low flows, high water temperatures, areas of difficult passage (as in precipitous canyons), or dams in rivers. Delay here is measured as days elapsing between release of tagged fish and subsequent observations at the counting boards. The delay also is assessed by comparing, at upstream points, the time of arrival of tagged fish released above and below the dam. The difference in time of arrival at an upriver point would be a measure of delay at the dam, and this difference should correspond to the delay observed at Rock Island Dam. It will be shown that this was true.

[2] An argument advanced is that studies of delays at dams should consider comparisons of travel rates before and after a dam is built. This has seldom been accomplished; subsequent to this study, comparisons of travel rates were made before and after Rocky Reach dam was built. Major, Richard L. and James L. Mighell. A study to measure delay to upstream migrating salmonids at Rocky Reach Dam. Manuscript. Bureau of Commercial Fisheries Biological Laboratory, Seattle, Wash.

RETURNS FROM UPSTREAM

Sockeye Salmon

It was necessary that days-out of tagged fish at upstream points be measured at a point where a minimum of mixing of (1) chronological order of movement and (2) delay might occur. Zosel Dam, on the Okanogan River, approximately 145 river miles above Rock Island Dam, appeared the best place for measuring the period of migration of tagged sockeye salmon. The sockeye passing this dam were headed for Lake Osoyoos and the spawning areas above the lake. They passed the dam easily, either through fishways or through the spillway. Unfortunately, not many tagged fish were released in the forebay at Rock Island in 1954, the year many sockeye and tags were observed at Zosel Dam. In 1955 and 1956, larger samples were released above the dam at Rock Island but most fish passed Zosel Dam unobserved. These data, at Zosel Dam, however, did allow us to compare the migration period of different lots of tagged fish.

Tumwater Dam on the Wenatchee River, the only other fish-passage observation point, presented a delay and mixing problem which precluded a reliable comparison of time periods for different tagged lots. At this dam, all fish had to find and ascend the ladder to pass the dam, and this offered chances for mixing and delaying of various parts of the salmon runs. The data obtained at Tumwater Dam are given for comparative purposes.

Figure 12 shows the days-out period at Zosel Dam for sockeye released at three areas at Rock Island. Looking at the modal values, we note a 2-day difference between forebay and left bank below the dam releases for both 1954 and 1955. The right bank modes, however, show a 3-day difference for 1954 and a 4-day difference for 1955. This would indicate right bank releases were delayed longer than left bank releases. The mean values do not indicate this difference between banks. Since the means are influenced by extreme values, however, the modal values should be preferred when making comparisons, provided the data are sufficient for forming smooth distribution curves. The number of observations leave something to be desired, but they indicate a delay of from 2 to 4 days at Rock Island, and a greater delay for right bank releases than left bank releases below the dam.

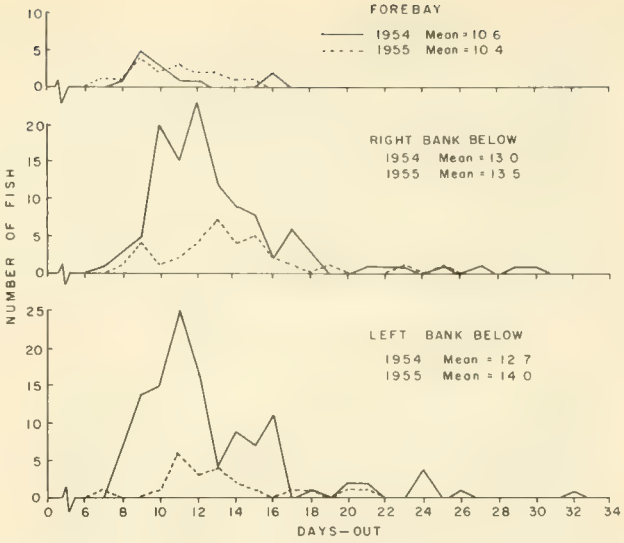


FIGURE 12.—Number of days out at Zosel Dam of tagged sockeye released at three different areas at Rock Island, 1954–55.

At Tumwater Dam, the difference in days-out between above- and below-dam experiments averaged 2 to 3 days in 1954 and 1955 (table 16). We observed that for these 2 years right bank releases took longer to pass than left bank releases. The 1956 results may have been affected by changed flow patterns at Tumwater Dam, the entire river was spilled over the dam and no water was diverted for power production as in previous seasons. The great range in individual days-out of tagged sockeye is indicated by the large standard deviations shown for the data.

Chinook

Our only upstream measure of the days-out period of tagged chinook salmon was obtained at Tumwater Dam. All other tag recoveries were from the spawning grounds or hatcheries,

TABLE 16.—*Means and standard deviations of days-out at Tumwater Dam of tagged sockeye released at different areas at Rock Island Dam, 1954–56.*

[Figures in parentheses are standard deviations]

Year	Release area at Rock Island Dam				Difference between above and total below
	Left bank below	Right bank below	Total below	Above dam	
1954	23.5 (7.3)	24.7 (7.0)	23.9 (7.2)	20.8 (5.9)	3.1
1955	21.6 (7.5)	22.1 (7.1)	21.8 (7.3)	19.9 (8.2)	1.9
1956	21.5 (8.0)	21.5 (9.4)	21.5 (8.4)	20.3 (7.9)	1.2

where the chronological order of the arrival of tagged fish could not be determined. At Tumwater Dam, moreover, migrating chinooks were subject to delay, and conclusive data of the time-out period for fish from the different tagging areas were not obtained. The days-out at Tumwater Dam for individual chinooks ranged from 11 to 65 days, and there was no evidence that any one group of releases was different from another group.

RETURNS AT ROCK ISLAND

Sockeye

As hypothesized previously, the difference in days-out at upstream points between above- and below-dam releases should equal the days-out period at Rock Island Dam of below-dam releases. The results at Rock Island Dam (fig. 13) confirm the hypothesis. The majority of fish passed through the fishways within 2 to 4 days after being released below the dam. In 1953, the peak of the days-out curve occurred a day earlier than in 1954-56. This may have been because the majority of fish in 1953 were tagged during a 3-day period near the end of the run in contrast to the season-long tagging of the later years.

The comparisons of days-out by area of release at Rock Island are shown in figures 14, 15, and 16. At first glance we have a fairly consistent picture of passage from the two areas of release, with the exception of the right bank releases in 1956. A better comparison of the days-out period for each release area is gained from the following

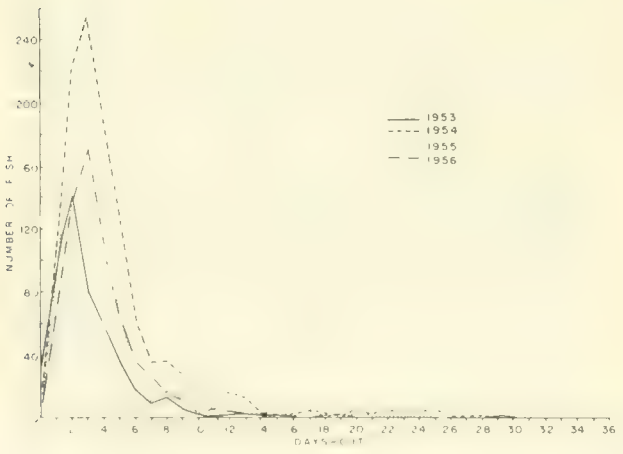


FIGURE 13.—Comparison of days-out at Rock Island of tagged sockeye released below the dam, 1953-56.

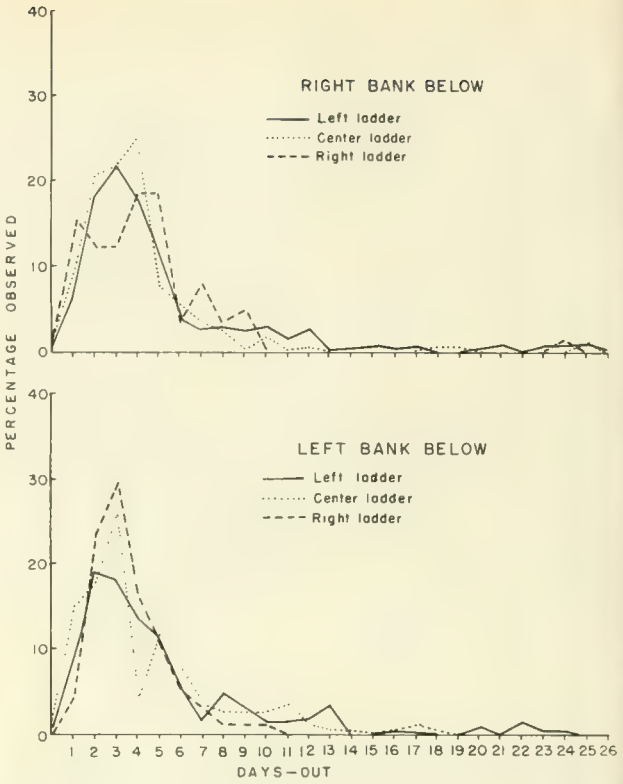


FIGURE 14.—Days-out of tagged sockeye at Rock Island for each area of release expressed in percentages of total observations by ladder, 1954.

array of modal values of days-out for each tag release area and the ladder of passage (table 17).

In 1954, right bank releases took a day longer to pass at each ladder than the left bank tag releases. This difference was not noted for other years except in 1955, in the center ladder. In 1956, right bank releases passed sooner than left bank releases. The 1956 tagged fish, it is recalled, were released off the face of the dam close to the fishways. Apparently the few sockeye using the right ladder moved into the ladder immediately after tagging and the remainder moved downstream or across the river. Those sockeye using the right ladder possibly moved up sooner upon finding the ladder because of the absence of resting areas below the ladder.

Measuring the number of days-out for tagged salmon at Rock Island Dam depended on the ability of the counters to distinguish the kinds and colors of tags used. As previously pointed out, the counters made many errors. To test if the counters were approximately correct in identi-

fying most tags upon which the days-out data were derived, the occurrence of tagged salmon, regardless of tag color or kind, was plotted by date and compared with the total number of salmon tagged (fig. 17). An examination of the graphs reveals that the peaks and troughs of the tag occurrence curve occur 2 to 4 days after the start and finish of a tagging period. This 2- to 4-day lag compares with the days-out curve of figure 13 and indicates the counters were approximately correct in identifying most of the tags from which the days-out data were derived.

TABLE 17.—*Modal values in days out for each tag release area and ladder of passage*

[Data from figs. 14, 15, and 16]

Releases	Ladder		
	Left	Center	Right
1954			
Left bank	2	3	3
Right bank	3	4	4–5
1955			
Left bank	3	2	2
Right bank	2	3	2
1956			
Left bank	3	2	3
Right bank	3	2	1

Undoubtedly the difference in time required for salmon released above and below Rock Island Dam to reach an upstream point reflects the amount of time required for the below-dam releases to pass the dam. Thus, it is reasonable to conclude that tagged sockeye were delayed 2 to 4 days below Rock Island Dam. Assuming that tagged and untagged salmon migrate at similar rates, Rock Island Dam delays sockeye approximately 2 to 4 days.

Chinook

At Rock Island Dam spring chinook peaked after 1 day-out and summer chinook on the third

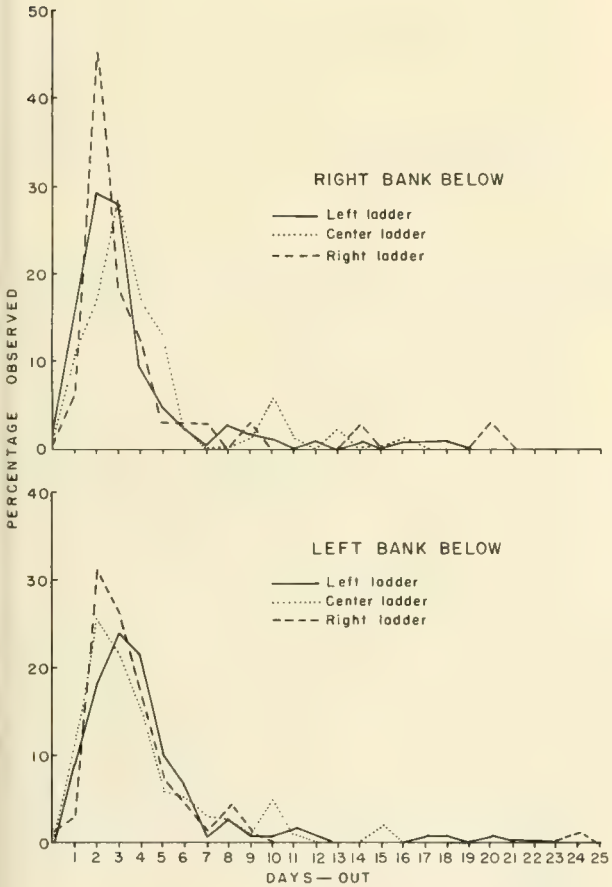


FIGURE 15.—Days-out of tagged sockeye at Rock Island for each area of release, expressed in percentages of total observations by ladder, 1955.

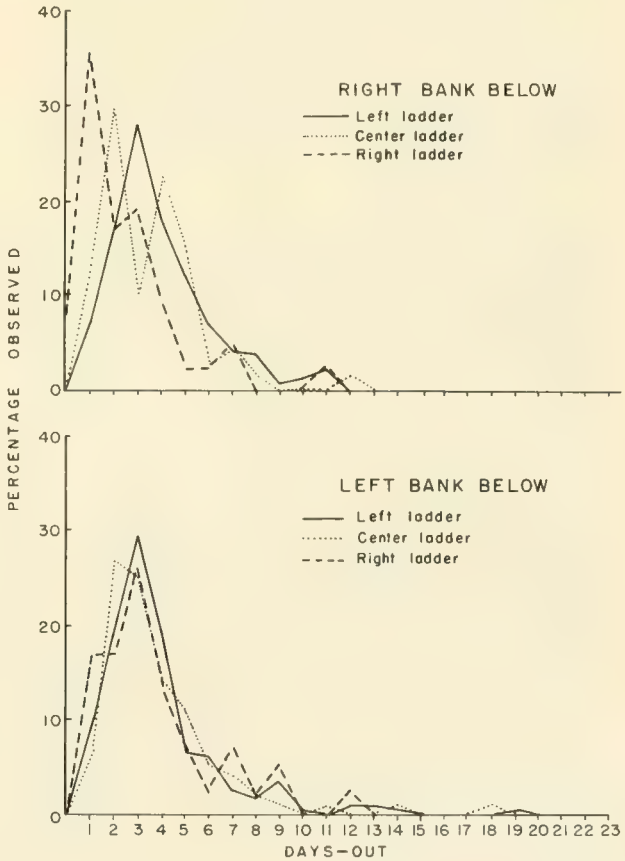


FIGURE 16.—Days-out of tagged sockeye at Rock Island for each area of release, expressed in percentages of total observations by ladder, 1956.

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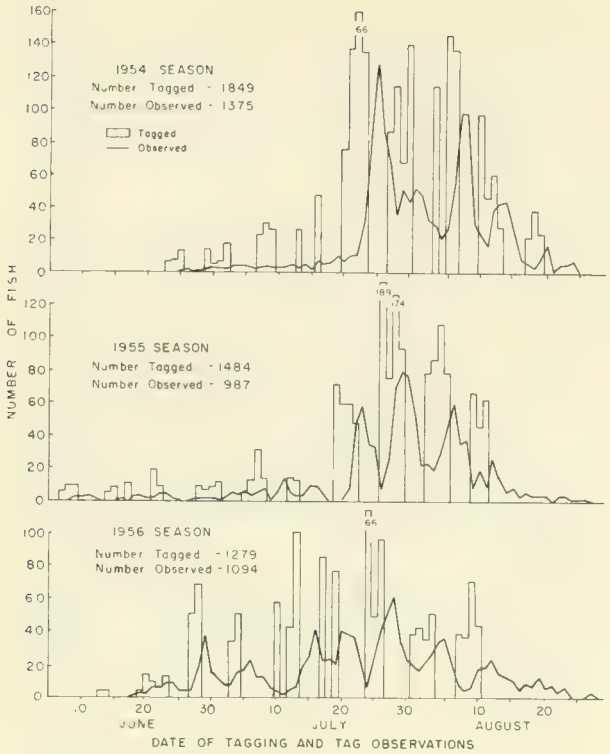

FIGURE 17.—Numbers of salmon tagged below Rock Island, and numbers of daily tag observations at the counting stations.

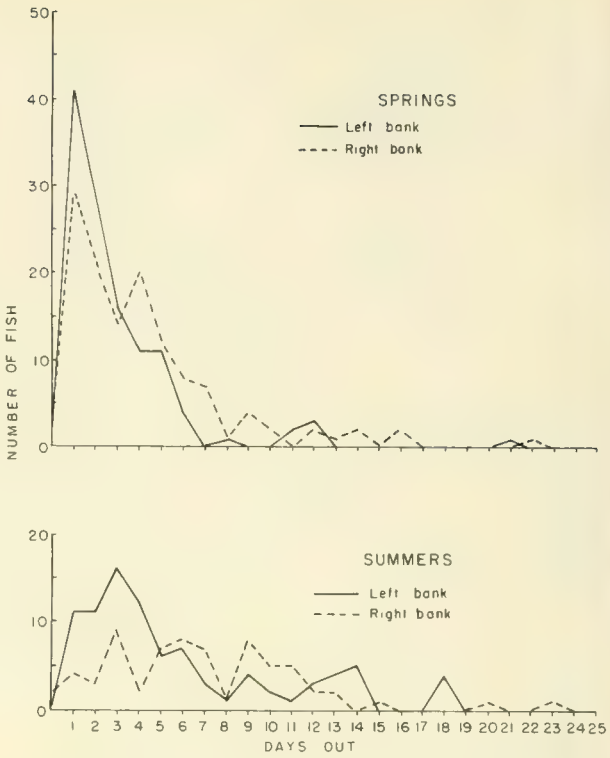

FIGURE 18.—Comparison of days-out at Rock Island of tagged spring and summer run chinook, by area of release, 1956 season.

day after tagging (fig. 18). The drawn-out time period noted for many summer chinooks may have resulted from errors in species identification as this run coincides with sockeye, or it may be characteristic of the summer chinook to take longer to pass the dam.

DISCUSSION

EXPERIMENTAL SITUATION

In view of conflicting results for different years and for different tagging areas, it is pertinent to review briefly the experimental situation and sources of error of the tagging experiments.

We have assumed that the likelihood of recovering or observing a tagged fish in a given recovery area was the same regardless of the area of release or time of tagging. This seems a reasonable assumption, because recovery efforts on spawning grounds were directed to all parts of the spawning areas and throughout the period of spawning. Tagged fish also were recorded as they passed Zosel Dam on the way to the spawning grounds, although sockeye could pass Zosel Dam without passing through counting traps. At Tumwater Dam, all fish, in order to pass the dam, had to pass through a trap where tagged fish were easily observed and counted.

We have assumed also that proportions of tagged fish migrating to different spawning areas were the same for the different release lots. In sampling fish for tagging, salmon were trapped throughout the duration of the run and usually during the height of the daily migration. In many instances, individual truck loads of fish were divided between above-dam and below-dam taggings. Other times, successive loads of fish were divided between left and right bank releases and above and below-dam releases. On this basis we feel that the above assumption is reasonable.

Another factor relating to experimental control was the kind of tag used for the various experiments. All the fish released above the dam were tagged with paired plastic disks. Different color combinations or single colors were used for different release groups. Tags used on fish released below the dam consisted of disks of single colors

in combination with plastic bars, nylon streamers, or vinyl tubing (spaghetti). Tags used below the dam were larger than the tags used above the dam. It might be argued that a larger, different shaped tag would aid recovery or observation of a tagged fish released below the dam. In considering the conditions for tag recoveries and observations, we do not agree with this argument. At Tumwater Dam all tags were observed in clear water from a distance of 3 or 4 feet. Most tags were read for numbers; thus, differentiation of tags from above and below the dam should have been readily apparent. This also holds true for tag observations at Zosel Dam. On the Okanogan River spawning grounds, tags were recovered from dead spawned-out fish or were observed during surveys of the river. In the latter case, biologists identified tags from 5 to 25 feet away and recognition was easy. In fact, when viewing tagged fish from the Tumwater Dam suspension bridge and from the railroad bridge just below Zosel Dam, both suspended 20 to 30 feet above the water, we could easily discern sizes and shapes of tags. Biologists observing fish at Rock Island distinguished, from about 40 feet away, shapes, sizes, and colors of tags on fish in the tailrace just below the fishway.

So far as tag colors are concerned, all tags used below the dam had single-colored disks and single-colored bars, streamers, or spaghetti. Tags used above the dam had single or bicolored patterns on the disks. It is difficult to say what the differences in colors or color combinations mean in terms of likelihood of recovery. Based on our observations of hundreds of tags under many circumstances, we believe that the tags, when seen, can be differentiated by color and kind.

ALTERNATIVE MODELS FOR ESTIMATING MORTALITY

Several models were considered for estimating mortalities in addition to the one used (ratios of recovery proportions of tagged fish from different release areas). We were unable, however, to accept the assumptions necessary for some. In others, dubious and conflicting results were obtained; hence, they are not given in detail in this paper. Two models are discussed briefly.

In one model we determined the racial composition of sockeye salmon in the tagged sample by estimating the number of 4-year-old upriver fish from the relative abundance of 3-year-old Okanogan fish in the tagged lots, and using the ratio of fishway counts to numbers released, as an adjustment factor in estimating the relative abundance of Wenatchee tagged fish in different release groups. Another model estimated racial composition from the differences in the proportions of 3-year-old sockeye in the populations at Rock Island Dam and in the Okanogan River, caused by a segment of the 4-year-old sockeye population splitting off and entering the Wenatchee system. In neither of these two models were definitive results obtained regarding mortalities caused by the dam. Mortalities were indicated for some years and areas, not for others. Because of these conflicting and nondefinitive results, we feel the best approach to the problem is that given.

MORTALITIES

Populations of anadromous salmonids lose some members passing large dams. For years, dead salmon have been observed floating down the Columbia River below Bonneville Dam, apparently fish which failed to pass the dam. Using the results of experiments involving the marking and recovery of dead salmon carcasses, Merrell and Collins [3] estimated a salmon loss at Bonneville Dam. Thompson (1945) found that a serious decline in Fraser River sockeye salmon runs was related to an area of difficult passage and to an obstruction in the river, even though salmon were known to pass this area each season. In a later paper on the Fraser River sockeye salmon, Talbot (1950) found that fish delayed longer than 14 days at Hells Gate did not reach their spawning grounds.

The tagging experiments at Rock Island gave conflicting results of mortalities caused by the dam. We found no mortalities for 3-year-old sockeye salmon when comparing recoveries of tagged fish released above and below the dam. We found mortalities in many experiments for 4-year-old sockeye when comparing tag returns from above and below dam releases. In other experiments involving these 4-year-old fish, no mortalities were indicated. Most experiments

[3] Merrell, Theodore R., and Melvin D. Collins. An investigation of adult chinook salmon mortality in the vicinity of Bonneville Dam, 1954 and 1955, on the Columbia River. Fish Commission of Oregon, August, 1960. 150 p. (Contract No. DA-35-026-eng-20892, U.S. Department of Interior, Fish and Wildlife Service.)

with chinook salmon indicated no mortalities caused by the dam.

Results show that mortalities caused by the dam are neither substantial nor consistent over the years, or that our tagging methods could not detect mortalities accurately. Confidence limits for the point estimates of mortalities ranged from zero (in many instances) to about 28 percent for the lower limits; upper limits ranged from 20 to 66 percent.

Comparatively few tagged fish used the right ladder (also observed for untagged runs), even when they were released near it. Apparently, the majority of these salmon ascended other ladders. An increased percentage of the salmon was attracted to the right ladder in 1957 when spillway gates on the right side of the dam were opened during the fish migration season. Previously these were closed to reduce water turbulence near the right ladder entrance. It may be that the added flow attracts fish to this bank and into the fishway.

While altering the right bank fishway might induce more fish to use the right ladder, we cannot say it would result in markedly improved facilities with respect to mortalities.

DELAY

Delay of migrating adult salmon runs is very important to the survival of the runs. As Thompson (1945) and Talbot (1950) pointed out, delays to sockeye salmon runs in the Fraser River caused mortalities and a serious decline in the runs. Schoning and Johnson (1956), in a study at Bonneville Dam on the lower Columbia River, reported that migrating chinook salmon were delayed 2.6 to 3 days. The 2- to 4-day delay at Rock Island Dam may not be important in itself, but if the delay is multiplied by a series of dams, serious losses of anadromous fish populations may result.

We do not know if upper river salmon runs would survive the series of delays in migration that may result when all Columbia River dams are completed. It may be that delays, if short-termed would be compensated for by easier and faster travel through the reservoirs created by the dams. These salmon do not spawn immediately upon reaching the spawning areas. There is an interval before spawning, of from 1½ to 2½ months after the salmon pass Rock Island Dam. This ripening period has been noted on other river systems. Howard (1948) found that the period for sockeye in Cultus Lake, British Columbia was about 1 month. Schaefer (1951) noted the time for sockeye in the Harrison River system of British Columbia, was a month or less. The ripening period for sockeye in Lakelse Lake, British Columbia, averaged 54 days (Fisheries Research Board of Canada, 1954). In the Bristol Bay area of Alaska, some sockeye remain in the lakes up to 3 months before spawning. The ripening period evidently is a necessary adjunct to the migration time.

In this study at Rock Island Dam, we discovered a 2- to 4-day delay to migrating salmon. Upstream tag observations at Zosel Dam indicated that fish tagged and released below the right ladder were delayed longer than fish tagged and released below the left ladder. This was confirmed by comparing returns of left and right bank tag releases at Rock Island for 1954. The longer delay was absent in 1955 and 1956. Thus, while we do not have positive evidence of a greater delay for fish released below the right ladder, such a delay is indicated.

Altering the right-bank fishway may lessen delay at the dam because of the possible increased chances of salmon finding a ladder sooner. However, the same delay pattern was noted at Bonneville Dam (app.), where ladders at both sides of the dam were designed to be equally attractive. From this study, we cannot conclude that altering the right bank fishway would decrease materially the overall delay at Rock Island Dam.

SUMMARY AND CONCLUSIONS

We conducted a tagging program at Rock Island Dam during 1953–56 to determine whether the dam caused loss or delay of salmon passing the dam, and whether such loss or delay was associated with the failure of fish to find and use the dam's right bank fishway. In this study, tagged salmon were released below the left and right bank fishways and above the dam. Fish counters at the dam identified different tag groups by noting the different colors and kinds of tags on salmon crossing the counting boards. Tags also were identified at upstream points on migration routes and during spawning surveys.

A comparison of upstream tag recoveries from the different release areas gave conflicting results regarding losses of fish. Point estimates of losses, for some combinations of years and release areas

(left or right bank below the dam), ranged from 0 to 42 percent, with mortalities greatest for fish released below the right bank ladder. Tagging data on chinook salmon indicated a loss of spring chinooks released below the right ladder in 1956; no loss was indicated, however, in comparing total returns from below the dam with returns from above the dam. For summer chinooks, tagging data failed to show losses due to the dam.

Total tag returns at Rock Island Dam, as identified by fish counters, ranged from 64 to 86 percent of the number released below the dam during the experiments. Straying and mortalities may have accounted for many of the missing tags; it was probable also that the counters missed many of the tags, and total returns were greater than indicated.

Tag returns at Rock Island Dam from below-dam releases showed that although salmon were released at both banks, the majority returned over the left ladder. Only 12 to 14 percent of the tagged salmon returned over the right ladder. The tag returns corresponded closely with the choice of ladders of the untagged populations, of which the majority chose the left ladder for passage and 10 to 17 percent the right ladder. Although the salmon were taken from the ladders for tagging, they did not learn a particlar route in re-passing the dam; neither were they frightened from a particular ladder during repassage of the dam.

Tagged salmon released above Rock Island Dam arrived at upstream points 2 to 4 days earlier than fish released below the dam. This difference in days out corresponded to the time required for most fish to pass Rock Island Dam after tagging, and is termed the delay at the dam. Fish released below the right ladder apparently were delayed 1 to 2 days longer in reaching upriver points than fish released below the left ladder.

The days-out period at Rock Island Dam, for sockeye released at the two banks below the dam, was essentially the same, with most of the salmon passing in 2 to 4 days, and the peak occurring the third day after tagging. In 1954, right-bank releases were delayed 1 day longer than left-bank releases. This greater delay of right-bank releases was not evident in 1955 and 1956. Spring chinook peaked after 1 day-out, with the majority passing the dam by the fourth day. The peak day for summer chinook was the third day after tagging. No apparent difference in days-out period at Rock Island Dam was indicated for chinooks released at the two banks below the dam.

An increased percentage of the run used the right ladder in 1957, following a change in spillway-gate operating procedures. Evidently attraction to this ladder was increased by opening gates on the right side of the dam next to the fishway.

On the basis of these tagging studies we found that Rock Island Dam delayed migrating salmon from 2 to 4 days. There is conflicting evidence of a greater delay to fish released below the right ladder than to fish released below the left ladder. Data regarding mortalities gave conflicting results; some experiments indicated substantial mortalities while others indicated none. While altering the right-bank fishway may attract more fish to the fishway, we cannot say it will necessarily improve passage considering overall loss and delay. The delay of 2 to 4 days may be significant when similar delays at a series of dams are considered.

ACKNOWLEDGMENTS

Many persons in addition to staff members at the Seattle Biological Laboratory contributed to the tagging experiments at Rock Island Dam. The Washington State Department of Fisheries helped in planning the project, and provided equipment for the investigations. The Puget Sound Power and Light Company, and Chelan County Public Utility District No. 1 gave valuable assistance by providing equipment and facilities. R. A. Fredin and D. D. Worlund of the Bureau's Biological Laboratory in Seattle assisted with the statistical analyses.

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APPENDIX

BONNEVILLE TAGGING EXPERIMENTS

At the conclusion of the Rock Island tagging experiments in 1954, we were confronted with the apparent loss at the dam of many tagged fish. What was the meaning of observing only approximately 75 percent of the tags released below the dam in 1954 and 64 percent in 1953? In the following years, 65 percent in 1955 and 86 percent in 1956 of all tags released were subsequently recorded by fish counters. Were these percentage returns due to conditions associated with the Rock Island fishways or could low percentage returns from tagging be expected at any dam? In an attempt to answer these questions we decided to tag, on a small scale, below another dam in the same manner as at Rock Island. The objectives were to determine the percentage and pattern of tag returns at Bonneville Dam and compare them with the Rock Island tagging data.

On July 14 and 15, 1955, 293 fish were tagged and released below Bonneville Dam located on the Columbia River approximately 140 miles above the river's mouth. The procedure at Bonneville was the same as at Rock Island. Fish were trapped in a ladder, transported by truck, and tagged and released below the dam. The experiments differed somewhat from those at Rock Island in that the fish were released about one mile below Bonneville on only one bank while at Rock Island they were released about, 1,000 feet below the dam at both banks. Also, fish at Bonneville were tagged with paired disks and not the combination tags applied at Rock Island.

TABLE A–1.—*Returns at Bonneville Dam of tagged salmon and steelhead released below the dam in 1955*

Species	Tagged	Returns by ladder			Returns No. tagged
		Washington shore	Bradford Island	Total	
	Number	*Number*	*Number*	*Number*	*Percent*
Sockeye	160	47	25	72	45.0
Chinook	17	9	30	[1] 39	229.4
Steelhead	116	36	16	52	44.8
Totals	293	92	71	163	
Percent by ladder		31.4	24.2	55.6	

[1] This is an obvious error in species identification.

Tag Returns at Bonneville

The number tagged and the returns at Bonneville are shown in table A–1. Far more steelhead were tagged at Bonneville than during the Rock Island experiments. Tag returns of 55.6 percent reported over Bonneville Dam by the fish counters were less than for any season at Rock Island, where percent returns ranged from 64 to 86 for the seasons 1953–56. Nine tags were returned from below Bonneville, six from dead fish found on the beaches and three from fishermen. At Rock Island the largest number of recoveries from below the dam occurred in 1956 when seven were recovered. Of these, five were from McNary Dam where a trap was installed for other tagging projects, one was returned by a sports fisherman, and one was observed in Redfish Lake in the Snake River system.

One feature found at Bonneville and not at Rock Island is the ship locks through which it is possible for fish to pass. There was no way of knowing whether or not any tagged fish passed the dam by this means.

As at Rock Island, the returns indicated fish counters had trouble identifying species. This is evident when 39 tagged chinook were reported by the counters and only 17 had been tagged. This same kind of error was noted at McNary Dam where fish counters reported 23 tagged chinooks from this same experiment.

The time-out period (time elapsing between tagging and observation at the counting boards) for tagged fish at Bonneville was similar to results obtained at Rock Island. Figure A–1 shows the number of days-out for all tagged fish observed at Bonneville. The majority of the fish passed in 2 to 5 days after tagging. There is an inherent error in the figure because days-out were computed from July 14, the first day of

tagging, although half the fish were tagged on July 15. There was no way for the counters to distinguish between the two lots. Correctly then, many fish passed 1 day sooner than indicated. It is notable that these results are similar to those from the Rock Island experiments in which the majority of fish passed in 2 to 4 days.

Figure A–2 shows the days-out by ladder at Bonneville. Many fish (44 percent) crossed the river to pass upstream through the Bradford Island ladder, although the fish were trapped and released on the Washington shore. The mean days-out time for fish passing through the two ladders was approximately the same: 6.6 days for the Washington shore ladder and 6.8 days for the Bradford Island ladder. Again, these results were similar to those obtained at Rock Island.

Tag Returns—Bonneville to McNary Dam

Tag recoveries were obtained above Bonneville Dam from the commercial fishery, sports fishermen, the Celilo Falls fishery, at McNary Dam, at Rock Island Dam, and also from spawning ground surveys above Rock Island. For the area between Bonneville and McNary Dams, 28 sockeye and 3 steelhead tags were returned by commercial fishermen and the Indian dip net fishery at Celilo Falls. Sports fishermen fishing in the various tributaries returned tags from seven tagged steelhead.

At McNary Dam, approximately 120 miles above Bonneville, 84 of the Bonneville tagged fish were recorded at counting stations. This was 28.7 percent of the number tagged and 51.5 percent of the number recorded over Bonneville Dam. The total number of tags accounted for from Bonneville to and including McNary counts was 122, or 41.6 percent of the number tagged and 74.8 percent of the number reported over Bonneville.

Figure A–3 shows the days-out for tagged fish at McNary Dam. The double mode is pronounced for each species and the modes are 5 days apart for chinooks and sockeye. It is doubtful that the 5-day interval is the result of computing days out from the first day of tagging when tagging occurred on 2 successive days. It is more likely that some short-term delay affected a group of fish, possibly those tagged the second day. The figure shows that the majority of tagged fish took from 12 to 20 days to pass McNary Dam after being tagged below Bonneville Dam.

Tag Returns Above McNary Dam

The Rock Island fish counters were alerted to the particular tag applied at Bonneville and recorded its appearance on fish. The tags used were paired disks of a copper color with a black bullseye, a very distinctive color, and much

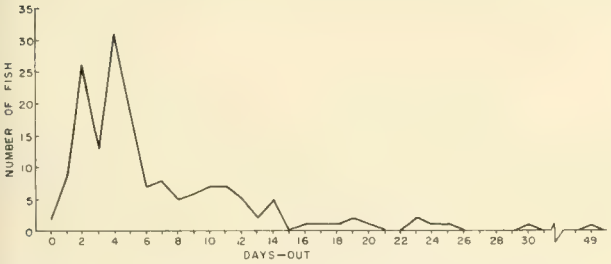

FIGURE A–1.—Number of days-out at Bonneville of tagged fish released below the dam, 1955 season (days-out dated from July 14).

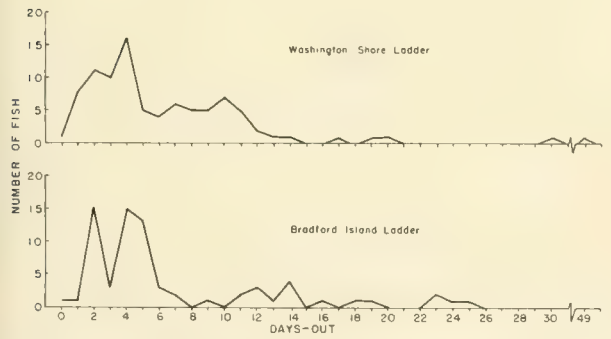

FIGURE A–2.—Number of days-out by ladder at Bonneville of tagged fish released below the dam in 1955 (days-out dated from July 14).

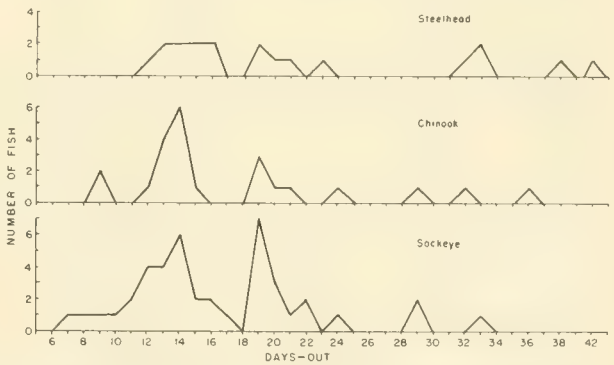

FIGURE A–3.—Number of days-out at McNary Dam for the three species tagged below Bonneville Dam in 1955 (days-out dated from July 14).

different from the tag combinations used below Rock Island. The counters reported five sockeye and one chinook tag of this group between August 3 and August 21. However, the counters were apparently unable to observe and identify this particular tag easily, for 14 tags (11 sockeye, 2 chinooks, and 1 steelhead) were recovered during spawning ground surveys above Rock Island.

If many of the Bonneville tags (8 of 14 or 57 percent) passed Rock Island undetected, where counters were alerted for tags of various colors and combinations, it is likely tagged fish could pass unnoticed at any dam. Unaccounted-for tags, which have been released below a dam, may not represent true mortalities of tagged fish occurring below a dam. These data are dependent upon the ability of fish counters to observe all tags, and for various reasons this may not be possible.

SUMMARY AND CONCLUSIONS

A small-scale tagging experiment below Bonneville Dam on July 14, and 15, 1955, and patterned after the Rock Island experiments, gave results similar to those obtained at Rock Island Dam. Total tag returns at Bonneville Dam were 56 percent, or somewhat less than the 64–86 percent returns at Rock Island for 1953–56. It is not known if tagged fish passed Bonneville by way of the navigation locks, thus reducing the number available for passage through the fishways. Fish released on one shore below Bonneville passed the dam through both fishways with only a slight majority passing through the Washington shore ladder on the side they were released.

The days-out period at Bonneville compared closely with the results obtained at Rock Island. The majority of tagged fish passed in 2 to 4 days at both dams. As at Rock Island Dam, the fish counters at both Bonneville and McNary Dams had difficulty in identifying species. More tagged chinooks were reported at Bonneville and McNary Dams than had been tagged.

The returns at Rock Island of the Bonneville releases were featured by the apparent inability of the counters to identify these tags. Six tags were reported at the dam and 14 were recovered on the spawning grounds above the dam. It is suggested, therefore, that tags may pass undetected at any dam and caution must be used in relating unaccounted-for tags to mortalities occurring below a dam.

OCCURRENCE IN TAMPA BAY, FLORIDA, OF IMMATURE SPECIES DOMINANT IN GULF OF MEXICO COMMERCIAL FISHERIES[1]

By James E. Sykes, *Fishery Biologist (Research Administration)*, and John H. Finucane, *Fishery Biologist (Research)*, Bureau of Commercial Fisheries

ABSTRACT

Populations of finfish, crabs, and shrimp were sampled from August 1961 through November 1962 as part of Tampa Bay estuarine studies. Specimens collected were identified to species and classified as immature or adult. Twenty-three species of major importance in Gulf of Mexico commercial fisheries were found to inhabit Tampa Bay during immaturity. Seasonal and areal distribution is described for the species common to Tampa Bay biological collections and catches in the Gulf. Although most of these species were distributed throughout the Bay system, Old Tampa Bay harbored greater numbers of them than any other area. Hillsborough Bay, an area of the system similar to Old Tampa Bay in salinity regimen, harbored fewer important species than any other area. Its relatively low production is attributed to loss of the natural habitat through human alteration. The role of the estuary in producing and rearing species important in Gulf fisheries is discussed, and the need for preservation of estuarine nursery areas is stressed.

It is becoming increasingly apparent that estuaries play an important role in the production of most finfish and shellfish harvested in coastal fisheries, and that civilization influences the nutrient capacity and productivity of these areas (Skud and Wilson, 1960).

Tampa Bay is one of the larger Gulf-connected estuaries, encompassing some 350 square miles. The primary purpose of this report is to enumerate and discuss species inhabiting this estuary in early life and entering Gulf fisheries as adults. The secondary purpose is to appraise relative species production between areas of the Bay as an aid in evaluating the probable effects on biota of the various engineering projects that are being proposed.

Man's ravages of estuarine areas in Florida are progressing so rapidly that many species of fish will disappear from these areas in the near future (Springer and Woodburn, 1960). Pollution and engineering projects are the greatest threat to the survival of estuarine species (Thompson, 1961, and Sykes, 1964 and 1965). These projects include harbor improvements, navigation channels, flood- and erosion-control structures, hurricane barriers, and fills to create new waterfront land. These alterations result in reduced water area. Adjacent bottom, including submerged grass flats, is destroyed by dredging, and the regimen of salinity and water temperature is changed. Sediments are added to the water, and damaging siltation occurs on nursery areas inhabited by commercial and sport fish species.

Although the danger to native aquatic animals is recognizable, the full significance of estuaries in the production and rearing of these organisms is not completely understood. Odum (1960) emphasized the importance of conducting research at both ends of the food chain to achieve a more complete understanding of ecological systems. He also implied that too many researchers start at a point well up on the food chain—fish, for instance—and work down. The East Gulf Estua-

Note.—Approved for publication November 11, 1964.

[1] Contribution No. 16, Bureau of Commercial Fisheries Biological Station, St. Petersburg Beach, Fla.

rine Investigations of the Bureau of Commercial Fisheries include studies of nutrients and primary crops of estuarine waters, as well as studies of the dependence of animals such as finfish, crabs, and shrimp upon nutrients and planktonic organisms (Sykes, 1965). The research, therefore, is being conducted near both extremes of the food chain and at intermediate points. Although the value of an estuary to our social and economic system should not be measured entirely in terms of its contribution to a commercial fishery, the harvest of edible and industrial species is a major consideration and is logically one of the factors motivating estuarine research. It was, therefore, important in our investigations to determine and study the important commercial species in Gulf of Mexico fisheries that utilize estuaries as rearing and developmental areas.

TAMPA BAY, WEST FLORIDA COAST, AND GULF FISHERIES

In evaluating the importance of Tampa Bay as a nursery area for commerical species, the size and economic value of commercial catches of the Gulf of Mexico should be considered.

Fisheries in the Gulf have grown notably in the past quarter-century. In 1936, 187 million pounds or 4 percent of recorded landings were from the Gulf; in 1961, this area yielded 1.3 billion pounds or 27 percent of total recorded U.S. fishery landings (Power, 1961). Of the average annual Gulf catch for 1958, 1959, and 1960, 12 percent (131,369,000 pounds) was landed on the west coast of Florida (Power, 1960, 1961, 1962a, 1962b). Size and value of the west Florida landings were second to Texas and exceeded Louisiana, Mississippi, and Alabama.

A summary of valuation showed that the total U.S. exvessel landings in the Gulf of Mexico were worth an annual average of $85 million for the 3 years cited. West Florida landings accounted for $20 million of that amount. Catches landed in the three counties surrounding Tampa Bay (Pinellas, Hillsborough, and Manatee) averaged 26 million pounds for the 3 years and accounted for $6 million of the total (U.S. Fish and Wildlife Service, 1959; Rosen, 1959; Rosen and Robinson, 1960). Pinellas County is dominant among the three counties in landings of seafood. It has the most extensive offshore commercial and sport fishing on the Florida west coast. The county supports the

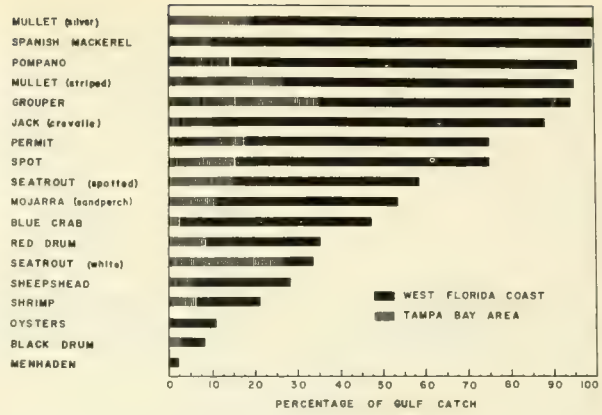

FIGURE 1.—Three year average (1958–59–60) of commercial landings on the Florida west coast and in Tampa Bay compared with total Gulf catches.

second largest fleet of commercial boats, the third largest fleet of party boats, and the sixth largest fleet of charter boats in the State (Moe, 1963).

Catch data were assembled for the important commercial species common to Gulf of Mexico, Florida west coast, and Tampa Bay fisheries (table 1). For a determination of percentages of the total Gulf catch landed on the Florida coast and in Tampa Bay (fig. 1), annual landings of these species were averaged for the three divisions of Gulf fisheries for the years 1958–60.[2] Two of the leading Gulf species, menhaden and oysters, were included even though their commercial catch in the Tampa Bay area was negligible.

More than 90 percent of the Gulf landings of silver mullet, spanish mackerel, pompano, striped mullet, and grouper were made on the Florida west coast (fig. 1). Annual landings of these species for 1958–60 averaged 12 million pounds in Tampa Bay, 45 million pounds on the west coast, and 47 million pounds in the Gulf. Species comprising 25–90 percent of Gulf catches landed on the west coast were crevalle jack, permit, spot, spotted sea trout, mojarra, blue crab, red drum, white sea trout, and sheepshead. Annual landings of these species for the 3 years averaged 1.5 million pounds in Tampa Bay, 19 million pounds on the west coast, and 38 million pounds in the Gulf. Landings on the west coast of the two most important commercial species in the Gulf (shrimp and menhaden) were each below 25 percent of total

[2] The species in table 1 and fig. 1 are listed according to percentage of Gulf catch landed on the Florida west coast rather than rank in the total Gulf catch.

TABLE 1.—*Average of 1958–60 annual landings of selected commercial species in Gulf of Mexico fisheries*

	Average Gulf landings	West Florida landings	Average 3-county [1] landings
	Pounds	*Pounds*	*Pounds*
Mullet (silver)[2]	690,300	690,300	137,900
Spanish mackerel	4,676,300	4,645,000	364,900
Pompano	506,700	486,000	66,200
Mullet (striped)	32,962,300	31,293,700	8,885,700
Grouper [2]	5,638,000	5,276,000	1,993,200
Jack (crevalle)	1,011,000	890,100	92,200
Permit	40,300	30,200	6,900
Spot	250,300	188,700	38,400
Sea trout (spotted)	4,817,700	2,821,300	652,300
Mojarra (sandperch)[2]	282,700	150,000	28,900
Blue crab	29,199,000	13,748,300	468,900
Red drum	2,009,300	712,100	152,900
Sea trout (white)	210,700	69,700	54,400
Sheepshead	378,000	107,200	23,900
Shrimp[2]	190,860,700	40,774,000	12,357,900
Oysters	13,409,000	1,380,300	1,900
Black drum	1,651,000	129,000	43,900
Menhaden [2]	678,523,000	11,092,600	4,000
Total	967,116,300	114,484,500	25,374,400

[1] Pinellas, Hillsborough, and Manatee.
[2] When several species were reported under a single common name by Federal and State statistical agents, they were listed accordingly regardless of the number of species involved.

Gulf catches. Oysters and black drum also were included in the 0–25 percent range. Average annual landings of these four species were 12 million pounds in Tampa Bay, 53 million pounds on the west coast, and 884 million pounds in the Gulf.

BIOLOGICAL COLLECTIONS

Monthly fish collections were made in the Tampa Bay area during August 1961 through November 1962. The study area encompassed the entire Tampa Bay system extending from the mouth throughout Old Tampa and Hillsborough Bays (fig. 2). The hydrological influence of the estuary extends into the Gulf for an undetermined distance; however, in this report only the semi-enclosed waters of Tampa Bay are regarded as estuarine habitat.

Gear used in collecting specimens consisted of 30-, 50-, and 70-foot minnow seines, a 10-foot shrimp trawl, a 16-foot balloon trawl, a 3 x 3-foot push net and a 6-foot cast net. Springer and Woodburn (1960) used similar seines, push nets, and, in addition, a roller frame trawl. In a qualitative assessment of the species occupying Tampa Bay and the sizes of these species, the collections by all types and sizes of gear were utilized and included in this report. When quantitatively describing occurrence by species and area, data were restricted to collections from the 10-foot shrimp trawl and the 50-foot seine. Duration of

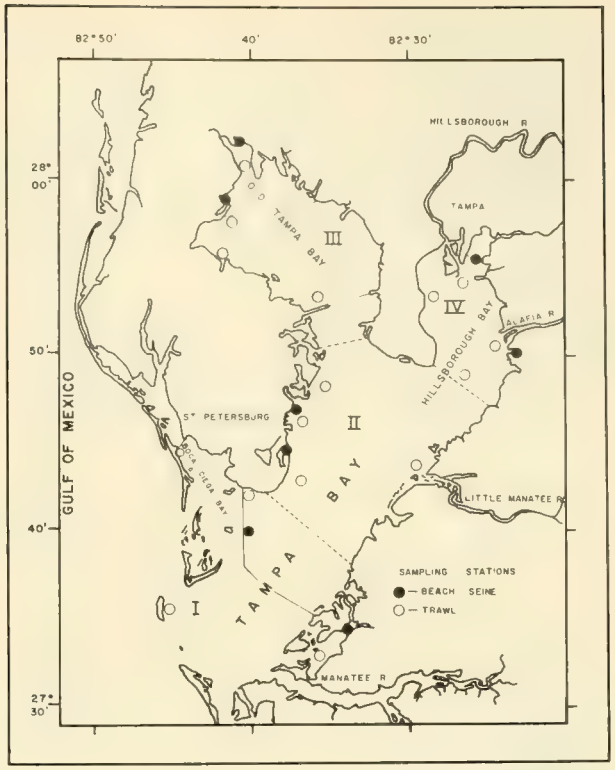

FIGURE 2.—Study areas and station locations in Tampa Bay.

each trawl haul was 10 minutes at 3–4 knots. Seine operation was as similar as possible at each station throughout the study period to insure comparability of results in catch per unit of effort.

Sampling stations were stratified throughout the Bay to collect specimens from the full salinity range. For comparison of species occupancy by area and salinity range, the stations were grouped to represent four areas based on salinity data from Saloman, Finucane, and Kelly (1964): Area I—lower Tampa Bay (salinity range, 21.92–37.16 °/₀₀, mean—31.95°/₀₀); Area II—central Tampa Bay (salinity range, 15.88–33.53°/₀₀, mean—24.48°/₀₀); Area III—Old Tampa Bay (salinity range, 0.09–31.83°/₀₀, mean—24.53°/₀₀); and Area IV—Hillsborough Bay (salinity range, 1.58–30.46°/₀₀, mean—23.63°/₀₀) (fig. 2).

The separation of specimens into immature or adult classes was based upon (1) observations of gonad development in relation to length frequency data compiled at the Bureau of Commercial Fisheries Biological Station at St. Petersburg, Beach, (2) published data on individual species

(Anderson, 1957; Anderson, 1958; Gunter, 1945; Guest and Gunter, 1958; Gunter and Christmas, 1960; Frisbie, 1961; Fields, 1962; Springer and Woodburn, 1960; and Rathbun, 1930), and (3) personal communication (Bonnie Eldred—Florida State Marine Laboratory, St. Petersburg, Fla. and George H. Rees—Bureau of Commercial Fisheries Biological Laboratory, Beaufort, N.C.).

Specimens were preserved in 10 percent formalin, and fish were measured to the nearest millimeter in standard length. The carapace of crabs (width) and shrimp (length) was measured by micrometer to the nearest one-tenth millimeter.

SUMMARIZED DATA

Fish and crustaceans from all stations and gear were classified as immature or adult to aid in assessing the utilization and dependency of each species on the estuary during early life. Although some adults were captured—and Tampa Bay sport fisheries take large numbers of them—specimens in sampling gear were limited largely to small forms. Size ranges and occurrence by section of Tampa Bay were noted (tables 2–5).

Trawl and seine catches of the commercially important finfish, shrimp, and crabs were compiled

TABLE 2.—*Size by season of commercial species of fish and crustaceans in Lower Tampa Bay—Area I, December 1961–November 1962*

Species	WINTER (Dec.–Feb.)				SPRING (Mar.–May)				SUMMER (June–Aug.)				FALL (Sept.–Nov.)			
	Immature		Adult		Immature		Adult		Immature		Adult		Immature		Adult	
	No.	Size range	No.	Size range	No.	Size range	No.	Size range	No.	Size range	No.	Size range	No.	Size range	No.	Size range
		Mm.		*Mm.*		*Mm.*		*Mm.*		*Mm.*		*Mm.*		*Mm.*		*Mm.*
Mugil curema (silver mullet)									14	51–107			2	114–121		
Mugil trichodon (silver mullet)	94	17–157			23	34–113			58	10–90			444	16–161		
Scomberomorus maculatus (spanish mackerel)									2	35–41			1	94		
Do													6	*133–158		
Trachinotus carolinus (pompano)									2	44–56			70	42–167		
Do									64	*23–87						
Mugil cephalus (striped mullet)	817	17–32			1,234	21–86	1	230	101	50–137			41	90–154		
Mycteroperca microlepis (gag)									5	160–263			15	160–195		
Epinephelus morio (red grouper)									2	84–92						
Caranx hippos (crevalle jack)	53	120–347							4	25–52			3	37–90		
Trachinotus sp. (permit)	1	150							20	21–83			69	35–109		
Do	9	*60–74							112	*8. 5–68. 5			76	*24–144		
Leiostomus xanthurus (spot)	888	12–147	37	151–175	823	21–143	29	150–175	47	61–142	12	150–175	10	94–130	38	147–248
Cynoscion nebulosus (spotted seatrout)	9	43–134			1	*5. 9			29	19–91	2	180–448	85	13–140	1	180
Eucinostomus gula (mojarra)	322	7–54	172	57–105	151	24–54	99	55–115	917	14–54	138	55–90	1,866	16–53	307	55–92
Eucinostomus argenteus (mojarra)	5	14–47	7	60–103	8	31–49	40	65–115	93	26–54	90	55–111	336	15–53	64	55–80
Diapterus plumieri (mojarra)	10	50–63							1	32			1	39		
Callinectes sapidus: (blue crab):																
Male	40	15. 1–82. 8	3	98. 0–140. 0	5	46. 0–80. 9	4	96. 3–150. 0	11	46. 0–89. 4	1	97. 3	97	12. 3–89. 0	6	103. 0–190. 0
Female	38	14. 8–95. 6	1	168. 0	10	42. 8–92. 1	1	138. 0	11	46. 4–95. 2			95	11. 7–96. 2	2	131. 0–202. 2
Sciaenops ocellata (red drum)	45	18–55	1	270	2	100–124							20	19–30		
Cynoscion arenarius (white seatrout)	1	75	8	180–225	2	27–50	6	175–210	11	25–75	12	166–206	20	16–165	23	172–223
Archosargus probatocephalus (sheepshead)	3	81–170	4	185–325	2	19–21	2	180–275	14	25–44			3	51–155	10	172–285
Penaeus duorarum (pink shrimp)	290	4. 8–20. 0	11	20. 5–26. 6	16	11. 1–19. 9	15	20. 7–28. 7	664	5. 2–18. 0			1,070	4. 3–20. 0	5	20. 2–24. 2
Pogonias cromis (black drum)							1	*593	2	116–128			1	170		
Brevoortia patronus (menhaden)					1	75			5	70–78						
Brevoortia smithi (menhaden)					2	25–76			3	71–75					3	135–185

*From Springer and Woodburn (1960).

TABLE 3.—*Size by season of commercial species of fish and crustaceans in Central Tampa Bay—Area II, December 1961–November 1962*

Species	WINTER (Dec.–Feb.)				SPRING (Mar.–May)				SUMMER (June–Aug.)				FALL (Sept.–Nov.)			
	Immature		Adult		Immature		Adult		Immature		Adult		Immature		Adult	
	No.	Size range	No.	Size range	No.	Size range	No.	Size range	No.	Size range	No.	Size range	No.	Size range	No.	Size range
		Mm.		*Mm.*		*Mm.*		*Mm.*		*Mm.*		*Mm.*		*Mm.*		*Mm.*
Mugil curema (silver mullet)	3	122–153							1	74						
Mugil trichodon (silver mullet)	53	28–143	7	175–234	7	121–137										
Scomberomorus maculatus (spanish mackerel)																
Trachinotus carolinus (pompano)																
Mugil cephalus (striped mullet)	187	18–24			157	24–71			16	53–87						
Mycteroperca microlepis (gag)																
Epinephelus morio (red grouper)																
Caranx hippos (crevalle jack)									2	25–45				*186–246		
Trachinotus sp. (permit)																
Leiostomus xanthurus (spot)	256	17–30			176	24–60			21	64–130	11	165–180	13	86–125	16	152–165
Cynoscion nebulosus (spotted seatrout)	3	52–86							11	18–132			54	27–80		
Eucinostomus gula (mojarra)	241	17–49	30	66–80	366	19–52	44	57–85	90	31–53	131	55–93	423	15–53	46	57–90
Eucinostomus argenteus (mojarra)	35	36–54	42	57–100	79	26–52	51	55–95	22	42–54	20	59–101	151	21–53	38	56–106
Diapterus plumieri (mojarra)													1	47		
Callinectes sapidus (blue crab):																
Male	4	13.3–46.8			3	46.0–63.0	3	92.0–144.0	10	12.7–78.0	5	90.0–113.5	25	14.3–69.0	2	135.0–154.5
Female	7	18.5–50.9			9	40.2–110.0			3	54.2–65.7			13	15.5–68.0	4	145.0–200.0
Sciaenops ocellata (red drum)	30	21–71			1	82							18	14–37		
Cynoscion arenarius (white seatrout)									15	14–125	12	165–200	1	35	12	184–227
Archosargus probatocephalus (sheepshead)					11	19–35			6	24–30			2	65–81		
Penaeus duorarum (pink shrimp)	27	6.3–15.1	2	29.7–31.8	3	12.8–16.0	1	23.2	334	5.3–19.5			422	5.0–19.7	1	20.3
Pogonias cromis (black drum)																
Brevoortia patronus (menhaden)																
Brevoortia smithi (menhaden)					2	31–36			1	*43.8					2	170–180

*From Springer and Woodburn (1960).

by month and area to compare abundance of immature animals (table 6). Catches included were from four selected trawl stations and two selected seine stations in each of the four sampling areas fished monthly. The catches of these six fishing operations in each area during 1 month represent one unit of effort. Thus, 72 hauls (12 standard units of effort) took place in each of the four areas during a 12-month period. The data allowed comparison of abundance between individual species by season and area (fig. 3). For this estimate, effort expended and numbers of specimens caught per species were combined for 3-month intervals; winter, spring, summer, and fall.

DISCUSSION

Most of the species landed by Gulf of Mexico commercial fisheries inhabit estuaries as immature, developing forms. It is assumed, therefore, that these estuaries are prime suppliers for the Gulf fisheries. Power (1962b) stated that five species—menhadan, shrimp, crabs, oysters, and mullet—comprised a catch of 1,131 million pounds or 89.3 percent of the Gulf commercial catch in 1960. Our investigations showed that 23 commercially important species including the dominant ones listed by Power (1962b) occupy Tampa Bay while immature.[3] All of these species are caught as

[3] Oysters are included in this number but were not collected by sampling gear.

TABLE 4.—*Size by season of commercial species of fish and crustaceans in Old Tampa Bay—Area III, December 1961–November 1962*

Species	WINTER (Dec.–Feb.)				SPRING (Mar.–May)				SUMMER (June–Aug.)				FALL (Sept.–Nov.)			
	Immature		Adult		Immature		Adult		Immature		Adult		Immature		Adult	
	No.	Size range	No.	Size range	No.	Size range	No.	Size range	No.	Size range	No.	Size range	No.	Size range	No.	Size range
		Mm.		*Mm.*		*Mm.*		*Mm.*		*Mm.*		*Mm.*		*Mm.*		*Mm.*
Mugil curema (silver mullet)					1	44			1	52						
Mugil trichodon (silver mullet)	60	15–101			7	41–134			49	22–84			159	15–101		
Scomberomorus maculatus (spanish mackerel)													1	*36		
Trachinotus carolinus (pompano)																
Mugil cephalus (striped mullet)	1,011	17–32	4	155–165	3,434	21–130			511	42–122			3	92–126	1	210
Mycteroperca microlepis (gag)																
Epinephelus morio (red grouper)																
Caranx hippos (crevalle jack)																
Trachinotus sp. (permit)																
Leiostomus xanthurus (spot)	1,279	12–135	17	151–157	3,170	21–139	15	149–190	486	40–137	20	155–189	262	66–133	61	150–185
Cynoscion nebulosus (spotted seatrout)	1	36–105	1	210	1	29	1	180	158	14–147	5	165–225	37	33–147	1	410
Eucinostomus gula (mojarra)	8	30–52	37	62–90			11	55–84	9	32–50	8	65–73	25	26–48	17	55–80
Eucinostomus argenteus (mojarra)	175	13–50	29	59–85	30	34–50	18	56–86	48	21–46	11	57–74	253	12–50	52	56–83
Diapterus plumieri (mojarra)	153	55–75							728	15–65	7	87–103	123	27–74		
Callinectes sapidus (blue crab):																
Male	40	12.3–88.0	8	93.6–195.0	47	40.0–88.7	16	90.5–180.0	19	39.0–87.0	59	92.0–140.0	30	18.0–83.5	38	90.5–163.0
Female	21	16.0–108.0	1	150.0	52	20.0–127.0	2	135.0–145.0	16	12.5–115.8	11	130.0–155.0	36	16.0–125.0	2	150.0–152.0
Sciaenops ocellata (red drum)	55	24–89			2	102–114							147	14–62		
Cynoscion arenarius (white seatrout)	6	55–140	2	192–198	6	35–49	3	210–258	307	17–95	6	155–195	164	20–118	4	160–215
Archosargus probatocephalus (sheepshead)	1	125			7	16–30			3	40–63			4	66–132	1	171
Penaeus duorarum (pink shrimp)	31	5.7–19.5	12	20.5–30.1	4	13.3–19.8	9	21.1–30.1	124	6.5–18.8	7	20.7–28.9	478	3.5–19.8	9	20.5–25.8
Pogonias cromis (black drum)									5	37–156			1	197		
Do					1,064	*20–75			57	*66–110						
Brevoortia patronus (menhaden)	1	*22.1			135	24–74			33	58–115			1	105		
Do									8	*55–108						
Brevoortia smithi (menhaden)					263	21–46			19	59–91						
Do						*19–29.1										

*From Springer and Woodburn (1960).

adults in Gulf of Mexico commercial fisheries and Tampa Bay sport fisheries. Few constitute important commercial fisheries in Tampa Bay. The significance of the estuary lies more in the growth of species for later harvest in Gulf fisheries than in catches of adults in nursery areas.

Shrimp comprise the most valuable fishery in the Gulf of Mexico (Power, 1962b). Commercial catches consist primarily of three species: the brown shrimp, *Penaeus aztecus;* the white shrimp, *P. setiferus;* and the pink shrimp, *P. duorarum* (Kutkuhn, 1962). Young of several species in developmental stages have been found in Tampa Bay (Eldred, Ingle, Woodburn, Hutton, and Jones, 1961)—the penaeid shrimp, *Trachypeneus constrictus* and *P. duorarum,* and the rock shrimp, *Sicyonia laevigata* and *S. typica.* These and one additional penaeid species, *Trachypeneus similis,* were identified in our collections (Saloman, 1964).

The important Gulf shrimp collected in Tampa Bay was *P. duorarum.* It is estimated that 75 percent of the shrimp brought to dock in the three-county area surrounding Tampa Bay are *P. duorarum* and 25 percent *P. setiferus.* Ninety-eight percent of the total is actually caught on the Campeche grounds (personal communication, Robert Benton—Bureau of Commercial Fisheries Biological Laboratory, Galveston, Texas). In Tampa Bay, *P. duorarum* is caught for a bait-shrimp market only. During October 1961

TABLE 5.—*Size by season of commercial species of fish and crustaceans in Hillsborough Bay Area IV, December 1961–November 1962*

Species	WINTER (Dec.–Feb.)				SPRING (Mar.–May)				SUMMER (June–Aug.)				FALL (Sept.–Nov.)			
	Immature		Adult		Immature		Adult		Immature		Adult		Immature		Adult	
	No.	Size range	No.	Size range	No.	Size range	No.	Size range	No.	Size range	No.	Size range	No.	Size range	No.	Size range
		Mm.		*Mm.*		*Mm.*		*Mm.*		*Mm.*		*Mm.*		*Mm.*		*Mm.*
Mugil curema (silver mullet)																
Mugil trichodon (silver mullet)	3	29–35			4	71–96							19	15–25		
Scomberomorus maculatus (spanish mackerel)															1	240
Trachinotus carolinus (pompano)																
Mugil cephalus (striped mullet)	10	19–100			83	22–88			63	56–115			4	121–153		
Mycteroperca microlepis (gag)																
Epinephelus morio (red grouper)																
Caranx hippos (crevalle jack)																
Trachinotus sp. (permit)																
Leiostomus xanthurus (spot)	12	18–30			367	27–137	18	158–176	25	70–135	3	155–175	3	95–110	12	145–165
Cynoscion nebulosus (spotted seatrout)	5	91–109							5	42–88			1	86		
Eucinostomus gula (mojarra)	2	19–53	3	75–85	1	42							1	43		
Eucinostomus argenteus (mojarra)	70	25–50	7	58–85	9	35–51	10	63–91	73	24–50	1	65	156	16–51	17	60–68
Diapterus plumieri (mojarra)	81	33–77	4	131–145					2	30–45			14	47–74		
Callinectes sapidus (blue crab):																
Male	7	40. 4–79. 6	1	166. 0	30	11. 0–80. 2	19	92. 0–153. 0	3	53. 2–87. 2	5	97. 1–149. 0	13	11. 8–87. 3	23	93. 0–163. 0
Female	6	28. 0–87. 2	2	132. 0–175. 0	19	42. 0–120. 0							7	20. 5–115. 0	1	164. 0
Sciaenops ocellata (red drum)	131	27–72											3	21–55		
Cynoscion arenarius (white seatrout)	11	114–153	4	170–221	14	18–45	10	170–210	29	17–83	1	181	36	17–142	36	166–248
Archosargus probatocephalus (sheepshead)	17	111–170			1	24			5	30–133			13	93–167		
Penaeus duorarum (pink shrimp)	18	10. 5–18. 4	12	29. 1–33. 5					3	9. 9–17. 4			47	5. 9–19. 4	10	20. 6–27. 3
Pogonias cromis (black drum)									16	48–114	1	278	1	165		
Brevoortia patronus (menhaden)					1	55										
Brevoortia smithi (menhaden)					7	23–28	1	241	179	33–69			2	87–93	2	159–172

TABLE 6.—*Numbers of immature specimens of fish and crustaceans taken in sampling gear by month, December 1961–November 1962, Tampa Bay, Fla.*

	Numbers of fish, shrimp, crabs				Total per month
	Area I	Area II	Area III	Area IV	
1961					
Dec.	54	22	103	35	214
1962					
Jan.	102	76	539	14	731
Feb.	315	414	627	36	1, 392
Mar.	182	261	1, 975	164	2, 582
Apr.	22	277	2, 016	254	2, 569
May	13	259	725	96	1, 093
Jun.	33	107	1, 028	260	1, 428
July	252	157	641	44	1, 094
Aug.	674	122	493	88	1, 377
Sept.	346	215	76	100	737
Oct.	325	531	249	36	1, 141
Nov.	227	258	116	88	689
Total per area	2. 545	2, 699	8. 588	1, 215	15, 047
Catch/unit effort	212. 1	225. 0	715. 7	101. 2	

through April 1962, 71,000 pounds of bait shrimp were caught in this fishery (Saloman, 1965).

Eldred et al. (1961) described recruitment of postlarval *P. duorarum* into Tampa Bay and a movement of larger shrimp from the Bay to offshore waters. Their observations on migration and our collections of larvae suggest that at least part of the Gulf shrimp fishery for that species depends upon populations developed in Tampa Bay.

Menhaden ranks first in size of catch and next to shrimp in value for all species landed in the Gulf of Mexico. The fishery in the Gulf depends upon catches of *Brevoortia patronus* (Gunter and Christmas, 1960). *B. smithi* and *B. gunteri* have been found in the Gulf, and probably comprise a very small fraction of the commercial catch.

There is no menhaden fishery in Tampa Bay, and landings of menhaden on the Florida west coast are minor in relation to total Gulf landings.

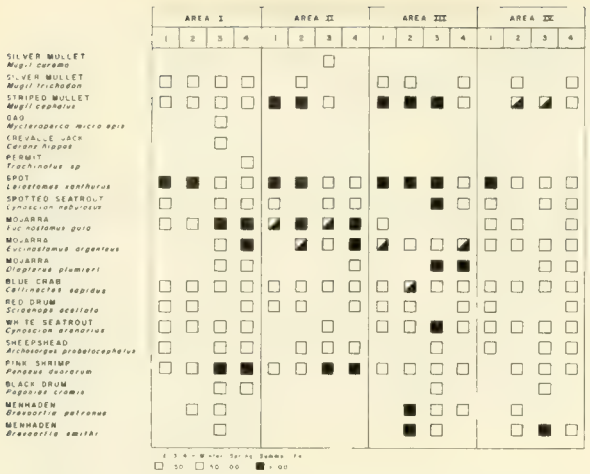

FIGURE 3.—Occurrence of immature commercial species of fish and crustaceans by season and area, Tampa Bay, Fla., December 1961–November 1962.

Gunter and Christmas (1960) and Reintjes (1961) observed that menhaden spawn at sea and subsequently move as larvae into estuaries which serve as nursery areas for further development. Collections in Tampa Bay by our staff and by Springer and Woodburn (1960) showed that Tampa Bay is a rearing area for two species of menhaden: *B. patronus* and *B. smithi*. *B. smithi* was more abundant and more widely distributed in our samples than *B. patronus;* the reverse of their occurrence in Gulf catches. Suttkus (1958) stated that *B. smithi* occurs in the eastern Gulf and that *B. patronus* overlaps *B. smithi* in the northeastern Gulf at Cedar Keys, Fla. Tabb and Manning (1960) reported only one species, *B. smithi,* from Florida Bay in the southern portion of the State. These findings suggest that normally *B. smithi* would be more abundant than *B. patronus* in central Florida or the Tampa Bay area.

Mullet ranked third in pounds landed in the Gulf and second both in Tampa Bay and on the Florida west coast. Heavy dependence upon the estuary was exhibited in that three species, *Mugil cephalus*, *M. trichodon*, and *M. curema*, were found in immature and adult stages. The striped mullet, *M. cephalus*, is dominant in Bay catches (Rosen and Ellis, 1958).

The blue crab, *Callinectes sapidus*, besides being prominent in Gulf fisheries, is harvested commercially in Tampa Bay. Also, it is the object of a large sport fishery. The species forms the most rapidly expanding fishery in Florida (Rosen and Robinson, 1960). Approximately 50 percent of the reported Tampa Bay landings (table 1) were actually caught in the Bay, and the remaining 50 percent were caught in Citrus County to the north of Tampa Bay and adjacent to the Gulf of Mexico.

C. sapidus was the dominant portunid in collections of metamorphosed and identifiable specimens. Numerous portunid zoeae and megalops also were taken. We were unable to make positive species identification at these stages and therefore cannot estimate the proportion of *C. sapidus* in the collections. Sandoz and Rogers (1944) stated that a salinity range of 23–30°/₀₀ is ideal for hatching blue crabs. Thus, from a salinity standpoint, the Bay appears to offer a favorable environment for hatching and development of blue crabs. This fact and the presence of adult blue crabs as well as portunid larvae led us to believe that the blue crab is reared within the confines of Tampa Bay. In addition to mature adults, the young identifiable metamorphosed forms (50-mm. carapace width) which inhabit the Bay are most abundant in winter.

The American oyster (*Crassostrea virginica*) is an estuarine resident and supports relatively small but growing commercial and sport fisheries in Tampa Bay. The actual harvest in the Bay is probably many times larger than the reported harvest (table 1). A portion of the beds is public, and fleets of small, privately owned boats tong for oysters there. In recent years, interest has been generated toward the possibility of increasing the numbers and sizes of the beds in Tampa Bay. Decreased oyster production in Chesapeake Bay has brought some oystermen into Florida from that area.

Of the 19 species of fish and crustaceans (fig. 3), 13 were taken in all four sections of Tampa Bay. This indicates that all of the Bay is used as a nursery area. Eighteen species were taken in the lower, high salinity portion of the Bay (Area I), 13 in the central portion (Area II), 15 in Old Tampa Bay where lowered salinities prevail (Area III), and 15 in Hillsborough Bay (Area IV), also an area of reduced salinity. The commercially important species of fish, shrimp, and crabs are euryhaline and, as expected, were distributed throughout the Bay system. The differ-

ences among numbers of species inhabiting sections of the Bay appeared to be of little or no consequence. This appraisal, however, is exclusive of those species not considered to be of commercial importance in this report.

Catch per unit of effort data made it possible to determine whether immature animals had a preference of habitat among areas of the Tampa Bay system (table 6). An overwhelming preference was apparent for Old Tampa Bay (Area III) where there were three times as many total animals as in either Lower or Central Tampa Bay (Areas I and II) and seven times as many as in Hillsborough Bay (Area IV). Abundance in Area III exceeded that of Areas I, II, and IV during 9 months out of 12. Although peak abundance varied between areas and time periods, March and April produced the greatest number of specimens per unit of effort from the collective areas.

Data on abundance of individual species by area and season also indicate an areal preference (fig. 3). Seven species were taken in numbers greater than 100 during at least one season (three units of effort) in Area III, five in Area II, four in Area I, and two in Area IV. The data indicate, therefore, that Area III (Old Tampa Bay) produces or develops more individuals during a greater portion of the year than any other area of the Tampa Bay system, and that Hillsborough Bay is the least productive of commercially important species.

Based on the known salinity preference of many euryhaline animals, it was expected that the greatest abundance of important species would be found in the low salinities of Old Tampa and Hillsborough Bays. Pearson (1929) and Gunter (1945, 1950) showed that a cycle of spawning, growth, and movement bore a distinct relation to salinity for many valuable fishes and invertebrates on the Gulf of Mexico coast. Salinity lower than that which is characteristic of the ocean is one of the requisites in early development of these animals. Abundance in Hillsborough Bay, however, was not nearly as great as in Old Tampa Bay. Because annual salinity patterns of Hillsborough Bay and Old Tampa Bay are similar, the difference in abundance of valuable species between the two areas must result from other environmental factors.

The introduction of industrial and domestic sewage is common in Hillsborough Bay. Natural flushing has not kept pace with the deposition of the effluents and has resulted in the accumulation of silt-size sediments throughout the Bay. Noxious compounds in solution, unstable and uninhabitable sediments, and insufficient dissolved oxygen appear to have contributed to a decline in Hillsborough Bay fisheries within a relatively short period of time.

As a nursery area for fish and crustaceans, Hillsborough Bay is no longer productive. Commensurate with alterations in bottom type and water quality, littoral areas which once supported a luxuriant growth of marine grasses are now barren except for the seasonal appearance of some red and blue-green algae.

In contrast, Old Tampa Bay remains in a relatively undisturbed state supporting blue crab, bait shrimp, and oyster fisheries, and serving as a nursery area for estuarine dependent fauna. Although industrial and residential interests continually threaten this area, it is vegetated with turtle grass (*Thalassia testudinum*), shoal grass (*Diplanthera wrightii*), cord or manatee grass (*Syringodium filiforme*), the red mangrove (*Rhizophora mangle*), and the black mangrove (*Avicennia nitida*) (Springer and Woodburn, 1960). The emergent vegetation aids in controlling the introduction of particulate detritus in surface water run-off before it enters the Bay.

Biologically, the water quality is good, and the predominantly firm sediment pattern creates a substrate suitable for the habitation of dense aggregations of benthic invertebrates. The stability of the bottom also promotes water clarity necessary for the existence of dense stands of marine algae and sea grasses which extend around the entire periphery of the area. The algae-sea grass ecosystem appears to be absolutely essential for survival and growth of juvenile stages of many commercially important species.

We conclude that the relatively undisturbed conditions of Old Tampa Bay and the fact that its salinity distribution is ideally suited to the development of many euryhaline fishes are responsible for its comparatively good productivity.

Many species recorded as inhabiting the estuary were omitted from our lists in this report. Some of these contribute indirectly but significantly to commercial fisheries by serving as food for marketable species. An example of an outstanding forage species is the scaled sardine (*Harengula pensa-*

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colae). It is produced in and inhabits the Tampa Bay area in great abundance throughout most of the year. The sardine is utilized heavily as a live bait in Tampa Bay and the adjacent Gulf areas. Other forage species abundant in the estuary are the tidewater silverside (*Menidia beryllina*), the bay anchovy (*Anchoa mitchilli*), the pinfish (*Lagodon rhomboides*), the thread herring (*Opisthonema oglinum*), and the silver perch (*Bairdiella chrysura*).

The number of species of finfish, shrimp, and crabs recorded from the Tampa Bay area now stands at 265 (Springer and Woodburn, 1960; Dragovich and Kelly, 1964). Most of these probably occupy an important ecological niche in the estuary and supply food to commercial and sport species of both Gulf and Bay. Obviously, a portion of the harvest of major fisheries in the Gulf is connected directly to the production and development of young forms in Tampa Bay. This is especially true of species found in catches of the eastern Gulf or on the Florida west coast. This estuary, of course, is not the only one important in the role of supplying Gulf fisheries. Sykes (1965) estimated that some 7,500 square miles or 4.8 million acres of estuarine area exist on the periphery of the Gulf.

The general public tends to view Tampa Bay either as an area of good but declining sport fishing or as an area for waterfront homesites. The present and future importance of Tampa Bay as a food source should be taken into account when proposals are filed for permission to enclose areas with bulkheads or create land masses in the estuary. This is especially true when such structures will divert currents, allow encroachment of high-salinity waters into upper areas, or otherwise significantly alter rearing areas of the species discussed.

SUMMARY

Biological collections showed that the five most important species in Gulf of Mexico commercial fisheries inhabit Tampa Bay in immature stages of development. Eighteen species of less importance in Gulf catches were also found in immature stages in the Bay. The qualitative distribution of species exhibited little difference between salinity range and area of the Bay system but numerically Old Tampa Bay, an area of relatively low salinity contained the greatest number of animals. The importance of Tampa Bay as a nursery area for species of fish, crustaceans, and mollusks comprising the most valuable portions of the commercial fisheries in the Gulf has not been stressed in the past. This role now must be recognized because of acceleration of engineering projects in the estuary that impair its value as a nursery ground.

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GILL NET MESH SELECTION CURVES FOR PACIFIC SALMON ON THE HIGH SEAS

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ABSTRACT

Gill net mesh selection curves of normal distribution were developed and applied to Pacific salmon caught by research vessels on the high seas of the North Pacific Ocean and the Bering Sea. Mesh selection curves were constructed for pink, sockeye, and chum salmon for each of four mesh sizes, 2½-, 3¼-, 4½-, and 5¼-inch. Catch efficiency curves for combined mesh sizes show that the range for salmon lengths was covered, although the coverage was not equal for all lengths. The length-frequency distribution of each species was adjusted for effect of gill net selectivity. Adjustments were minor.

The Bureau of Commercial Fisheries fishes experimentally for salmon with surface gill nets on the high seas of the North Pacific Ocean and the Bering Sea. Salmon samples taken by gill nets are used to estimate abundance, distribution, racial identity, and growth of salmon populations in the ocean. Accurate estimates of abundance, distribution, racial identity, and growth require unbiased samples from salmon populations in the ocean. Gill nets are selective; a particular mesh size of gill net selects a particular size range of fish.

To cover the range of fish sizes, four gill net mesh sizes, 2½-, 3¼-, 4½-, and 5¼-inch, stretched measure, of multifilament nylon twine are used in the fishing. Selectivity studies are necessary to assess the adequacy of this coverage and to adjust the salmon size frequencies for any bias caused by selectivity. Determining the shape and extent of the mesh selection curve for each mesh size and for combined mesh sizes is necessary before size frequencies can be adjusted for possible bias.

Note.—Approved for publication June 25, 1964.

A METHOD FOR DETERMINING GILL NET SELECTIVITY

Holt (1957) described a method for determining gill net mesh selection curves with normal frequency distributions. He developed normal mesh selection curves for Fraser River sockeye salmon (from Peterson, 1954) and for North Sea herring (from Hodgson, 1933). He used the ratio of catches from adjacent pairs of mesh sizes at different length classes to develop parameters for the normal curve. The following formulations were abstracted from Holt (1957) and McCombie and Fry (1960):

$$C_L = nP_L p_m \cdot e^{-(L-L_m)^2/2S^2} \qquad (1)$$

where C_L is the number of fish of length L caught, n the number of operations or the fishing duration, P_L the number of fish of length L liable to capture, p_m the fishing power of the mesh at the mean selection length, e the base of natural logarithms, L_m the mean selection length caught, and S the standard deviation of distribution. The ratio of catches for two meshes (A and B), differing slightly in size and fishing together, can be de-

scribed by an equation of the linear form, $y=bL+a$:

$$\log \frac{{}_BC_L}{{}_AC_L} = \frac{({}_BL_m - {}_AL_m)\cdot L}{S^2} + \frac{{}_AL^2{}_m - {}_BL^2{}_m}{2S^2} + \log \frac{B^P{}_m}{A^P{}_m} \quad (2)$$

in which ${}_BC_L$ is the catch of length L taken in mesh B, ${}_BL_m$ is the mean selection length of mesh B, $B^P{}_m$ is the fishing power of mesh B, etc. The log $\frac{B^P{}_m}{A^P{}_m}$ term will cancel; i.e., log 1=0, by assuming that the two nets have equal fishing power for their respective mean lengths. If the terms from equation (2) are used, $\log \frac{{}_BC_L}{{}_AC_L}=y$, $\frac{{}_BL_m - {}_AL_m}{S^2}=b$ (the slope), and $\frac{{}_AL^2{}_m - {}_BL^2{}_m}{2S^2}=a$ (the y intercept). When equation (2) holds true, a plot of $\log \frac{{}_BC_L}{{}_AC_L}$ against various values of L gives a straight line, and the assumption is justified that the mesh selection curve is normal.

The selection curve parameters, ${}_AL_m$, ${}_BL_m$, and S, are obtained as follows:

$$a/b = \frac{{}_AL_m{}^2 - {}_BL^2{}_m}{2S^2} \Big/ \frac{{}_BL_m - {}_AL_m}{S^2}$$

$$-2a/b = {}_BL_m + {}_AL_m$$

Assume that L_m is proportional to mesh size (θ). Assign a proportionality constant (K). Then, ${}_AL_m + {}_BL_m = -2a/b = K({}_A\Theta {}_B\Theta)$, from which ${}_AL_m$ and ${}_BL_m$ can be derived. S can be found from either a or b. With these values and a table of ordinates for normal distribution (Snedecor, 1956), mesh selection curves can be constructed.

APPLICATION OF METHOD TO SALMON GILL NET CATCHES

I have applied the above analytical procedure to length frequencies of three salmon species: pink, sockeye, and chum. To illustrate the method, I have used catch data for 1957 and 1959. In these years the three species were well represented in the gill net catches of the research vessels. Catch data on sockeye and chum salmon for 1956, 1958, and 1960 were used in part of the analysis. Table 1 shows the number of the three species caught and measured during 1956 to 1960. The catches were made during May to September on the high seas of the North Pacific Ocean (north of lat. 45° N.) and the Bering Sea.

PINK SALMON

Table 2 gives the length-frequency distributions of pink salmon taken by the 3¼-, 4½-, and 5¼-inch mesh gill nets in 1957. Table 3 gives similar data for 1959. Catches were confined to three mesh sizes; the 2½-inch mesh did not catch pink salmon. Since more of the 4½-inch mesh than of the 3¼- and 5¼-inch meshes was used in a fishing set, catches of the 4½-inch mesh were reduced to equalize fishing effort. A 1:3 reduction was necessary in 1957; a 1:6 reduction in 1959. Length frequencies were grouped by 3-cm. length classes. Fork length is related to mesh size.[1]

Tables 2 and 3 also give catch ratios of adjacent mesh sizes, 4½/3¼-inch and 5¼/4½-inch. The catch ratio at each length class is limited to a combined sample size of 50 or more fish for the paired mesh sizes. By establishing a minimum sample size of 50, I was able to omit smaller samples that may not have been representative

TABLE 1.—*Gill net catches of pink, sockeye, and chum salmon by U.S. research vessels in the North Pacific Ocean and the Bering Sea, 1956–60*

Species [1]	Number of salmon caught and measured				
	1956	1957	1958	1959	1960
Pink	431	3,129	174	4,202	1,049
Sockeye	3,224	3,584	1,177	6,462	8,296
Chum	3,565	4,678	3,744	6,082	5,816

[1] Coho and chinook salmon are excluded because of small catches.

TABLE 2.—*Catch by mesh size and catch ratio of adjacent mesh sizes, pink salmon, 1957*

Fork length (midpoint of length class)	Catch by mesh size [1]				Catch ratio	
	2½-inch	3¼-inch	4½-inch	5¼-inch	log 4½/3¼-inch	log 5¼/4½-inch
Centimeters	*Number*	*Number*	*Number*	*Number*		
35		2				
38		14	1			
41		148	69	1	−0.76	−4.27
44		192	363	13	+.64	−3.32
47		42	300	32	+2.00	−2.24
50		3	109	47	+3.51	−.84
53		1	19	22		
56			8	5		
59		1	1	1		

[1] Original catches of the 4½-inch mesh were 3 times as large as shown; they were divided by 3 to equalize fishing effort between mesh sizes.

[1] Mesh size as shown is factory-labeled size. During the 1960 fishing operations about 400 meshes from the four mesh sizes were measured. The average measured size was either identical to the factory-labeled size or slightly oversize.

TABLE 3.—*Catch by mesh size and catch ratio of adjacent mesh sizes, pink salmon, 1959*

Fork length (midpoint of length class)	Catch by mesh size [1]				Catch ratio	
	2½-inch	3¼-inch	4½-inch	5¼-inch	log 4½ / 3¼-inch	log 5¼ / 4½-inch
Centimeters	*Number*	*Number*	*Number*	*Number*		
32		1				
35		3				
38		7				
41		38	26		−0.39	
44		16	201	6	+2.53	−3.51
47		6	236	14	+3.67	−2.83
50		1	135	51	+4.90	−0.97
53		1	46	49		+0.07
56		1	14	30		
59			3	3		
62		1		3		

[1] Original catches of the 4½-inch mesh were 6 times as large as shown; they were divided by 6 to equalize fishing effort between mesh sizes.

The natural logarithm of the catch ratio is directly related to the length of pink salmon for 1957 and 1959 (fig. 1). The straight lines are fitted by the least squares method. The relation in both years is approximately linear. Holt showed in equation (2) that this relation must be linear if the mesh selection curve is normal. With replicating evidence for 2 years, I feel justified in assuming that the mesh selection curve for pink salmon is approximately normal.

To obtain the normal frequency curve for each mesh size, the mean selection length and the standard deviation of the curve were needed. The estimation of these parameters for 1959 pink salmon is shown in table 4 and the determination of the normal curve in table 5.

A further step in applying the method was to construct a composite selection curve from the mesh selection curves of the three mesh sizes (fig. 2). This composite curve was obtained by summing at each length class the ordinate heights of the individual curves (table 6), as was done by McCombie and Fry (1960). The composite curve can be called a "catch efficiency curve" because

TABLE 4.—*Estimation of mean selection length and standard deviation of mesh selection curves, pink salmon, 1959*

Mesh sizes	Sum of mesh sizes	Sum of mean selection lengths (−2a/b)	Mean selection length	Standard deviation of selection curve
	Centimeters	*Centimeters*	*Centimeters*	*Centimeters*
3¼-inch (8.26 cm.)			34.8	
3¼ and 4½-inch	19.69	81.36		4.9
4½-inch (11.43 cm.)			48.1	
4½ and 5¼-inch	24.77	105.65		4.4
5¼-inch (13.34 cm.)			56.2	
Mean	22.23	93.50		

$K = 93.50/22.23 = 4.21$.

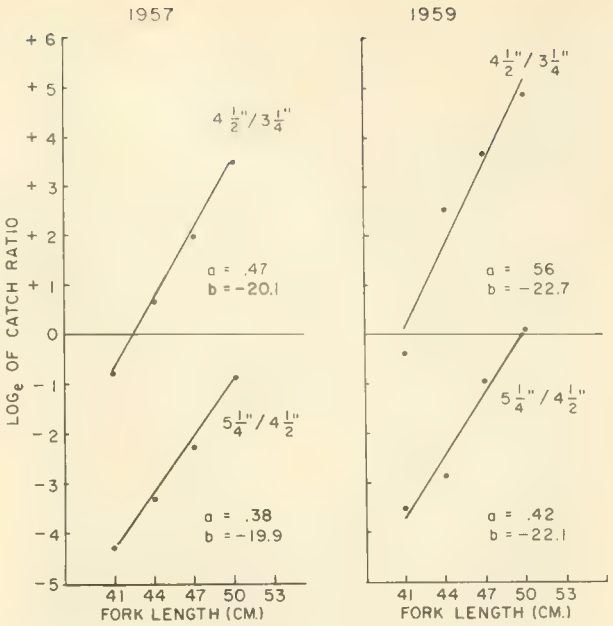

FIGURE 1.—Catch ratio of adjacent mesh sizes by fork length, pink salmon, 1957 and 1959.

TABLE 5.—*Determination of ordinate heights of normal curve for each mesh size, pink salmon, 1959*

Fork length (midpoint of length class)	3¼-inch mesh L_m=34.8, S=4.9 [1]		4½-inch mesh L_m=48.1, S=4.6 [2]		5¼-inch mesh L_m=56.2, S=4.4	
	$\frac{L-L_m}{S}$	Ordinate height	$\frac{L-L_m}{S}$	Ordinate height	$\frac{L-L_m}{S}$	Ordinate height
Centimeters						
32	0.57	0.339	3.50	0.001		
35	.04	.399	2.85	.007		
38	.65	.323	2.20	.036	4.23	0
41	1.27	.178	1.54	.122	3.55	.001
44	1.88	.068	.89	.268	2.77	.009
47	2.49	.018	.24	.388	2.09	.045
50	3.10	.003	.41	.367	1.41	.148
53	3.71	0	1.07	.225	.73	.306
56			1.72	.091	.05	.398
59			2.37	.024	.64	.325
62			3.02	.004	1.32	.167

[1] L_m=mean selection length (cm.), S=standard deviation (cm.).
[2] Mean of 4.9 and 4.4.

TABLE 6.—*Summation of ordinate heights of three mesh selection curves, pink salmon, 1959*

Fork length (midpoint of length class)	Ordinate height (by mesh size)			Sum of ordinate heights
	3¼-inch	4½-inch	5¼-inch	
Centimeters				
32	0.339	0.001		0.340
35	.399	.007		.406
38	.323	.036	0	.359
41	.178	.122	.001	.301
44	.068	.268	.009	.345
47	.018	.388	.045	.451
50	.003	.367	.148	.518
53	0	.225	.306	.531
56		.091	.398	.489
59		.024	.325	.349
62		.004	.167	.171

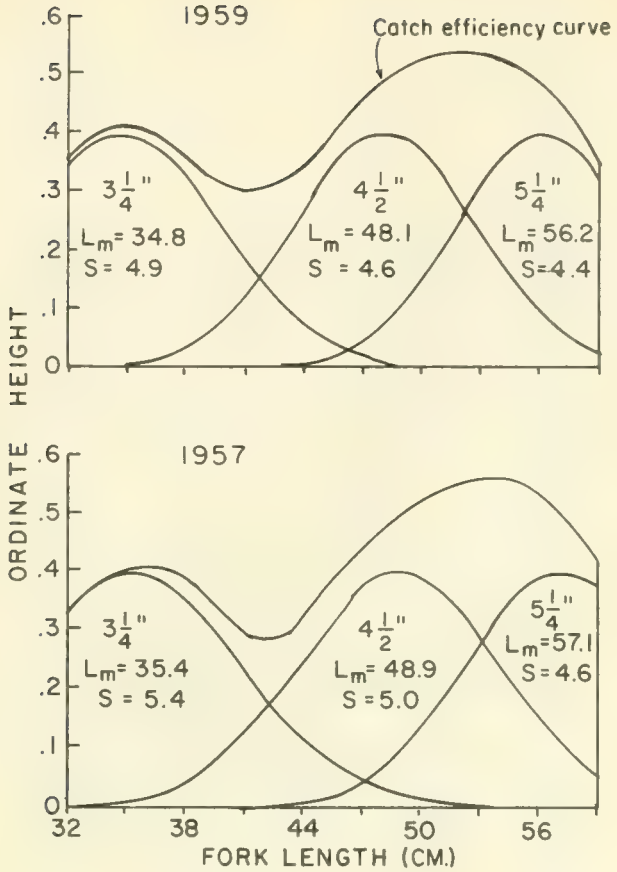

FIGURE 2.—Catch efficiency curve (sum of ordinate heights at each length) for three mesh sizes combined, pink salmon, 1957 and 1959.

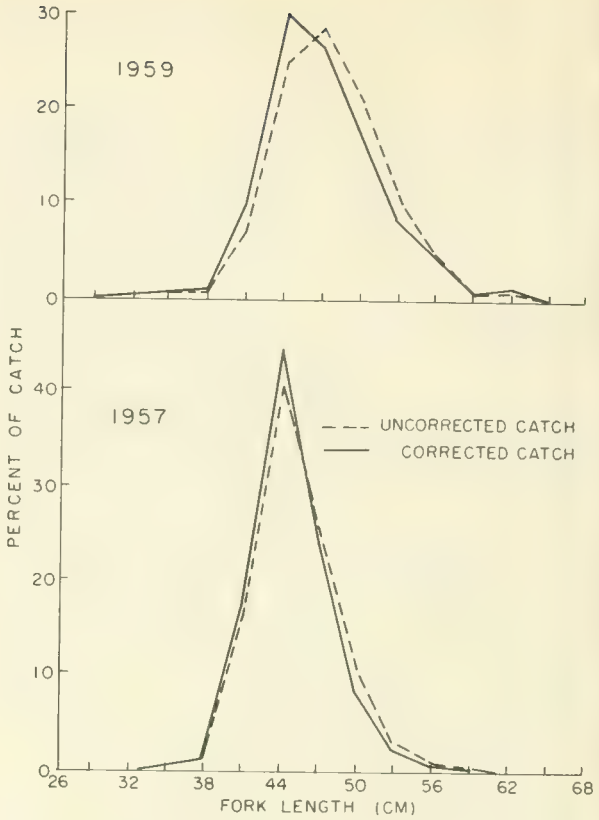

FIGURE 3.—Length frequency distribution of pink salmon adjusted for effect of gill net selectivity, 1957 and 1959.

it shows a relative catch efficiency of gill nets over fish length range. Curves for 1957 and 1959 are shown.

In both years the catch efficiency curves show a dip at 41 cm. Catch efficiency at 41 cm. is lower because of the 1¼-inch gap between the 3¼- and 4½-inch mesh sizes. The gap between the 4½- and 5¼-inch meshes is ¾ inch.

The final step in applying the method was to reconstruct the length frequency curve of the available fish population, adjusting for effect of gill net selectivity. The uncorrected catch was divided by the sum of ordinates at each length class (table 7). The corrected catch for all length classes was the length frequency curve adjusted for effect of gill net selectivity.

When the uncorrected and the corrected length frequency distributions of pink salmon taken by combined mesh sizes of gill net in 1957 and 1959 are plotted, a single mode of maturing 2-year-old fish is evident (fig. 3).

Adjustments for gill net selectivity in 1957 were minor. In the uncorrected catches the 41-cm. and 44-cm. length classes were slightly under-represented and the 47-cm., 50-cm., and 53-cm. classes were slightly over-represented. The corrected catch curve adjusts for these conditions. The mode, after I adjusted for selectivity, remains unchanged at 44 cm.

In 1959 the amount of correction was somewhat greater than in 1957. As in 1957, the 41-cm. and 44-cm. lengths were under-represented, the 47-cm., 50-cm., and 53-cm. lengths over-represented. Adjustments in 1959 changed the position of the mode from 47 cm. to 44 cm.

SOCKEYE SALMON

Least squares lines were fitted to the catch ratios of sockeye salmon taken in 1959 by the four gill net mesh sizes (fig. 4). Catch data are in table 8. Catch ratios were computed for

TABLE 7.—*Adjustment of 1959 catches of pink salmon for effect of gill net selectivity*

Fork length (midpoint of length class)	Uncorrected	Sum of ordinate heights	Corrected	Uncorrected	Corrected
Centimeter	*Number*		*Number*	*Percent*	*Percent*
32	1	0.340	3	0.1	0.1
35	3	.406	7	.3	.3
38	7	.359	19	.8	.9
41	64	.301	213	7.2	10.0
44	223	.345	646	25.0	30.3
47	256	.451	568	28.7	26.7
50	187	.518	361	21.0	16.9
53	96	.531	181	10.8	8.5
56	45	.489	92	5.0	4.3
59	6	.349	17	.7	.8
62	4	.171	23	.5	1.1

samples of 50 or more fish, as was done for pink salmon. Sockeye salmon catch ratios for each pair of mesh sizes showed approximate linearity over the greater part of the range of fish lengths, but not at the extremes of the range. Approximate linearity extended from 29 cm. to 38 cm. for the 3¼/2½-inch mesh sizes, from 38 cm. to 53 cm. for the 4½/3¼-inch mesh sizes, and from 47 cm. to 62 cm. for the 5¼/4½-inch mesh sizes. Least squares lines were fitted in these ranges. The procedure of discarding extremes in line-fitting previously was used by Garrod (1961).

Figure 5 shows a similar picture for 1957 (data are in table 9). Catch ratios were approximately linear except at the extremes. In 1957 and 1959 similar length ranges were used in line-fitting, except for extending the range to 41 cm. for the 3¼/2½-inch mesh sizes in 1957.

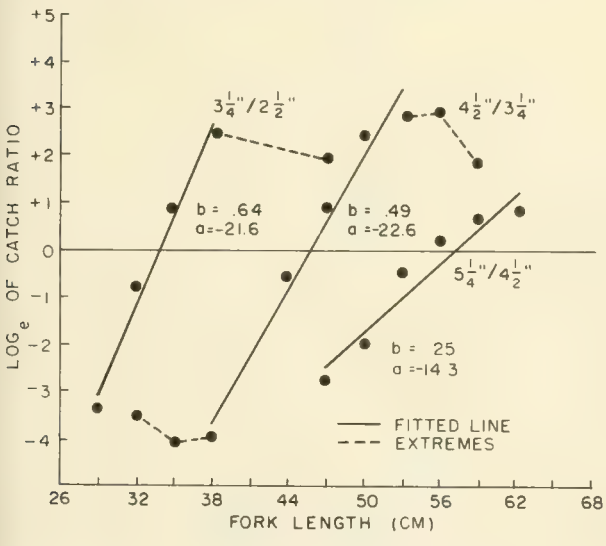

FIGURE 4.—Catch ratio of adjacent mesh sizes by fork length, sockeye salmon, 1959.

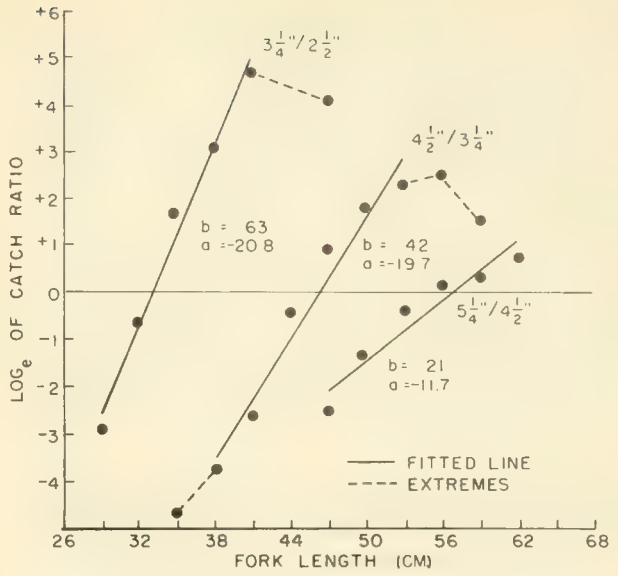

FIGURE 5.—Catch ratio of adjacent mesh sizes by fork length, sockeye salmon, 1957.

TABLE 8.—*Catch by mesh size and catch ratio of adjacent mesh sizes, sockeye salmon, 1959*

Fork length (midpoint of length class)	Catch of sockeye by mesh size [1]				Catch ratio		
	2½-inch	3¼-inch	4½-inch	5¼-inch	log 3¼/2½-inch	log 4½/3¼-inch	log 5¼/4½-inch
Centimeters	*Number*	*Number*	*Number*	*Number*			
26	9						
29	88	3			−3.38		
32	293	139	4	4	−.75	(−3.54)	
35	279	648	9	7	+.85	(−4.27)	
38	22	268	5	2	+2.50	−3.96	
41	1	34	2			−2.85	
44	1	41	23	2		−.58	
47	6	44	111	7	(+1.99)	+.92	−2.76
50	1	16	161	23		+2.40	−1.94
53	3	9	155	97		+2.84	−.47
56		9	118	144		(+2.94)	+.19
59	3	9	59	116		(+1.88)	+.68
62		6	22	51			+.82
65	2	4	4	22			
68	1		1	5			
74				1			

[1] Original catches of the 4½-inch mesh were 6 times as large as shown; they were divided by 6 to equalize fishing effort between mesh sizes.

NOTE.—Catch ratios in parentheses were not used. See text.

Catch ratios showing the linear relation represent mainly fish which were enmeshed (gilled) around the head and gill cover by the net twine. Catch ratios departing from the straight line at either end were discarded because they represent large fish snagged or small fish tangled in the gill nets.

In the 1959 sockeye catch ratios of the 4½/3¼-inch mesh sizes (fig. 4), the discarded catch ratios at 32 cm. and 35 cm. and at 56 cm. and 59 cm. curve away from the fitted line, giving the effect of a tipped S-shaped curve. At 32 cm. and 35 cm. the fish in the 4½-inch mesh were probably

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TABLE 9.—*Catch by mesh size and catch ratio of adjacent mesh sizes, sockeye salmon, 1957*

Fork length (midpoint of length class)	Catch of sockeye by mesh size [1]				Catch ratio		
	2½-inch	3¼-inch	4½-inch	5¼-inch	log 3¼/ 2½-inch	log 4½/ 3¼-inch	log 5¼/ 4½-inch
Centimeters	*Number*	*Number*	*Number*	*Number*			
23	4						
26	36	1					
29	55	3			−2.90		
32	54	29	1	1	−.62		
35	32	168	2	1	+1.66	(−4.62)	
38	8	176	4	1	+3.09	−3.77	
41	1	108	8		+4.68	−2.60	
44		46	31	3		−.40	
47	1	57	133	11	(+4.04)	+.85	−2.49
50	3	34	194	50		+1.74	−1.36
53	4	15	146	100		+2.28	−.38
56	3	9	108	121		(+2.48)	+.11
59	3	20	84	114		(+1.44)	+.31
62	2	11	26	54			+.73
65		4	6	20			
68	1	1	1	1			
71				1			

[1] Original catches of the 4½-inch mesh were 3 times as large as shown; they were divided by 3 to equalize fishing effort between mesh sizes.

NOTE.—Catch ratios in parentheses were not used. See text.

tangled rather than gilled. At 56 cm. and 59 cm. the fish in the 3¼-inch mesh were mainly snagged rather than gilled. Some fish within the 38-cm. to 53-cm. length range also were snagged or tangled, but the numbers were so small that the linear relation between fish length and log of catch ratio was unaffected.

The procedure for developing mesh selection curves and a catch efficiency curve for sockeye

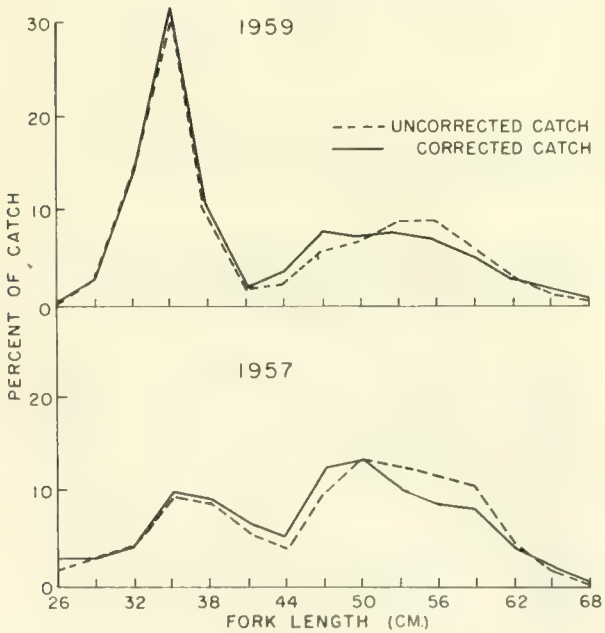

FIGURE 6.—Length frequency distributions of sockeye salmon adjusted for effect of gill net selectivity, 1957 and 1959.

salmon followed that for pink salmon. Table 10 shows the summation of the ordinate heights of the mesh selection curves for the four mesh sizes. The composite curve was used to adjust for selectivity effect (table 11).

A comparison of the uncorrected and corrected length frequency distributions of sockeye salmon in 1957 and 1959 shows that the 44-cm. and 47-cm. fish are under-represented, the 53-cm. to 59-cm. over-represented in the uncorrected catches (fig. 6). Over most of the length range, adjustments were quite minor.

Adjustments for the effect of gill net selectivity changed slightly the shape of the length-frequency distribution curve of sockeye salmon. The length-frequency distributions in 1957 and 1959 were bimodal. Mode 1 consisted of small fish (highly abundant in 1959) that had spent one winter at sea. Mode 2 consisted of large fish that

TABLE 10.—*Summation of ordinate heights of four mesh selection curves, sockeye salmon, 1959*

Fork length (midpoint of length class)	Ordinate height (by mesh size)				Sum of ordinate heights
	2½-inch	3¼-inch	4½-inch	5¼-inch	
Cm.					
26	0.268	0.013			0.281
29	.398	.056			.454
32	.306	.165	0		.471
35	.122	.319	.003		.444
38	.025	.391	.014	0	.430
41	.003	.327	.049	.001	.380
44	0	.176	.124	.005	.305
47		.062	.242	.019	.323
50		.014	.357	.060	.431
53		.002	.398	.142	.542
56		0	.337	.259	.596
59			.216	.365	.581
62			.106	.398	.504
65			.039	.335	.374
68			.011	.218	.229

TABLE 11.—*Adjustment of the 1959 catches of sockeye salmon for effect of gill net selectivity*

Fork length (midpoint of length class)	Uncorrected	Sum of ordinate heights	Corrected	Uncorrected	Corrected
Centimeter	*Number*		*Number*	*Percent*	*Percent*
26	9	0.281	32	0.3	0.5
29	91	.454	201	2.9	2.9
32	440	.471	944	14.2	13.8
35	943	.444	2,158	30.5	31.4
38	297	.430	678	9.6	9.9
41	37	.380	97	1.2	1.4
44	67	.305	218	2.2	3.2
47	168	.323	525	5.4	7.6
50	201	.431	472	6.5	6.9
53	264	.542	491	8.5	7.2
56	271	.596	455	8.8	6.6
59	187	.581	321	6.0	4.7
62	79	.504	156	2.6	2.3
65	32	.374	85	1.0	1.2
68	7	.229	30	.2	.4
74	1	(.044)			

NOTE.—Length class 74 cm. was omitted.

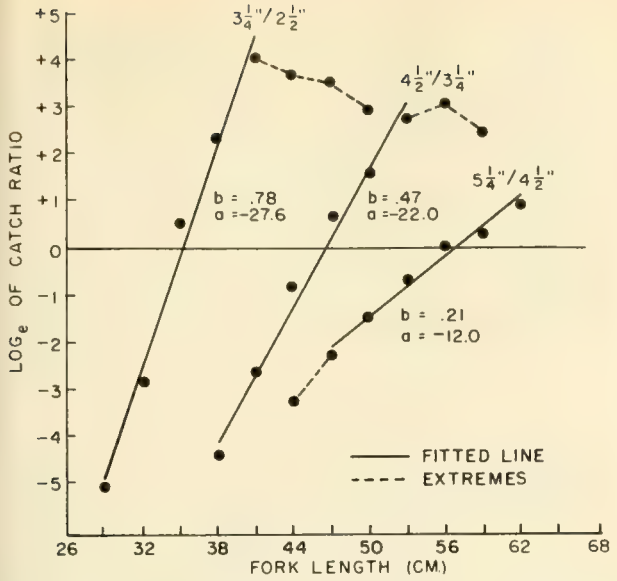

FIGURE 7.—Catch ratio of adjacent mesh sizes by fork length, chum salmon, 1957.

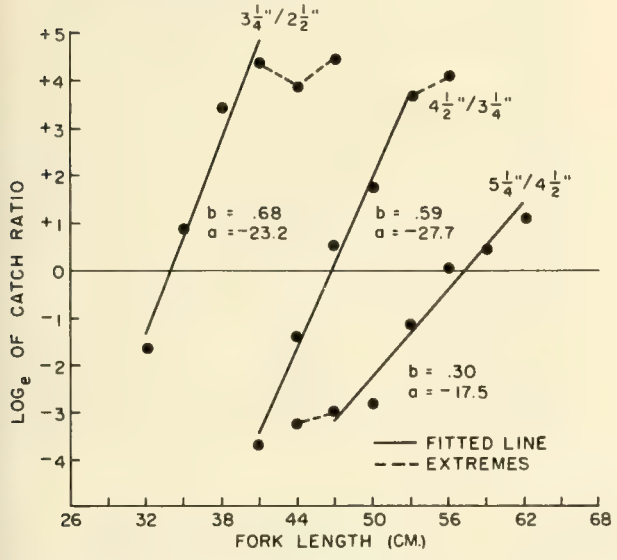

FIGURE 8.—Catch ratios of adjacent mesh sizes by fork length, chum salmon, 1959.

had spent mainly two and three winters at sea. Mode 1 did not change position, but mode 2 shifted to smaller fish when adjusted for selectivity. This change occurred in both years.

Chum salmon

The problems encountered for chum salmon and the results obtained are almost identical to those for sockeye salmon. As with sockeye, chum salmon catch ratios of a minimum 50-fish sample

TABLE 12.—*Catch by mesh size and catch ratio of adjacent mesh sizes, chum salmon, 1957*

Fork length (mid-point of length class)	Catch of chum by mesh size [1]				Catch ratio		
	$2\frac{1}{2}$-inch	$3\frac{1}{4}$-inch	$4\frac{1}{2}$-inch	$5\frac{1}{4}$-inch	log $3\frac{1}{4}$/$2\frac{1}{2}$-inch	log $4\frac{1}{2}$/$3\frac{1}{4}$-inch	log $5\frac{1}{4}$/$4\frac{1}{2}$-inch
Centimeters	*Number*	*Number*	*Number*	*Number*			
26	5						
29	330	2	1	1	−5.12		
32	523	28		2	−2.92		
35	52	89		1	+.54		
38	8	78	1		+2.28		
41	2	109	8		+4.00		
44	3	119	52	2	(+3.68)	−0.83	(−3.27)
47	3	100	191	21	(+3.50)	+.65	−2.21
50	3	58	285	64	(+2.96)	+1.59	−1.49
53	1	13	203	105		+2.75	−.66
56		6	117	105		(+2.97)	−.01
59	1	4	46	66		(+2.44)	+.36
62			16	41			+.94
65			5	15			
68			2	10			
71				1			
74				1			

[1] Original catches of the $4\frac{1}{2}$-inch mesh were 3 times as large as shown; they were divided by 3 to equalize fishing effort between mesh sizes.

NOTE.—Catch ratios in parentheses were not used. See text.

TABLE 13.—*Catch by mesh size and catch ratio of adjacent mesh size, chum salmon, 1959*

Fork length (mid-point of length class)	Catch of chum by mesh size [1]				Catch ratio		
	$2\frac{1}{2}$-inch	$3\frac{1}{4}$-inch	$4\frac{1}{2}$-inch	$5\frac{1}{4}$-inch	log $3\frac{1}{4}$/$2\frac{1}{2}$-inch	log $4\frac{1}{2}$/$3\frac{1}{4}$-inch	log $5\frac{1}{4}$/$4\frac{1}{2}$-inch
Centimeters	*Number*	*Number*	*Number*	*Number*			
29	9						
32	57	11		1	−1.64		
35	18	44	1		+.89		
38	3	93		1	+3.42		
41	2	156	4		+4.36		
44	4	196	48	2	(+3.89)	−3.65	(−3.22)
47	1	84	160	8	(+4.43)	−1.41	−3.00
50	1	37	232	14		+.53	−2.81
53	2	5	195	67		+1.78	−1.08
56		2	113	116		+3.66	+.03
59			59	95		(+4.03)	+.50
62		2	14	45			+1.17
65			4	24			
68				4			
71				2			

[1] Original catches of the $4\frac{1}{2}$-inch mesh were 6 times as large as shown; they were divided by 6 to equalize fishing effort between mesh sizes.

NOTE.—Catch ratios in parentheses were not used. See text.

for each pair of mesh sizes were approximately linear over a greater part of the range of fish lengths but not at the extremes. The length ranges for chum salmon were identical to those established for sockeye. Least squares lines were fitted to the 1957 and 1959 catch ratios of the three pairs of mesh sizes (figs. 7 and 8). Catches on which these lines were based are given in tables 12 and 13. Table 14 sums up the ordinate heights for the four mesh sizes.

Figure 9 and table 15 show the uncorrected and corrected length-frequency distributions of chum

TABLE 14.—*Summation of ordinate heights of four mesh selection curves, chum salmon, 1959*

Fork length (midpoint of length class)	Ordinate height (by mesh size)				Sum of ordinate heights
	2½-inch	3¼-inch	4½-inch	5¼-inch	
Cm.					
26	0.242	0.006			0.248
29	.393	.033			.426
32	.319	.122	0		.441
35	.130	.280	.001		.411
38	.026	.395	.005		.426
41	.003	.341	.024	0	.368
44	0	.180	.078	.001	.259
47		.060	.187	.007	.254
50		.012	.323	.030	.365
53		.001	.398	.091	.490
56		0	.352	.201	.553
59			.223	.331	.554
62			.102	.398	.500
65			.033	.352	.385
68			.008	.228	.236

salmon. In 1957 and 1959 the corrected catches increased at 44 cm. and 47 cm. and decreased at 53 cm. to 59 cm. As with sockeye, the mode of the large chum salmon shifted to smaller fish when adjusted for selectivity.

SELECTIVITY COMPARED FOR THE THREE SPECIES

The catch efficiency of the combined mesh sizes was compared for pink, sockeye, and chum salmon (fig. 10). Curves were given for sockeye and chum salmon ranging in length from 29 cm. to 62 cm. and for pink salmon from 38 cm. to 56 cm.; these covered 98 percent of the samples. Chum and sockeye curves are similar and show a dip in catch efficiency at 44 cm. and 47 cm., resulting from the

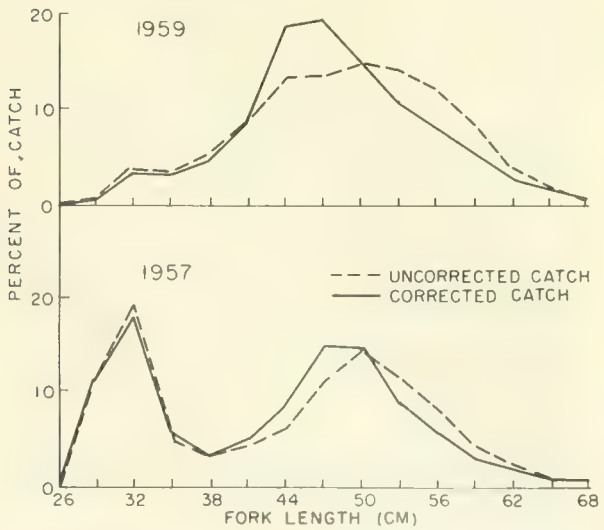

FIGURE 9.—Length frequency distribution of chum salmon adjusted for effect of gill net selectivity, 1957 and 1959.

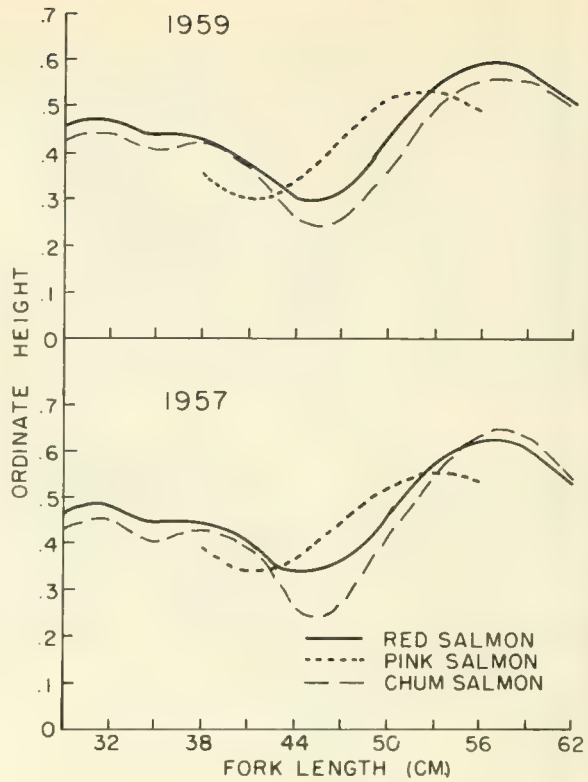

FIGURE 10.—Comparison of catch efficiency of combined mesh sizes on pink, sockeye, and chum salmon, 1957 and 1959.

TABLE 15.—*Adjustment of the 1959 catches of chum salmon for effect of gill net selectivity*

Fork length (midpoint of length class)	Uncorrected	Sum of ordinate heights	Corrected	Uncorrected	Corrected
Centimeters	*Number*		*Number*	*Percent*	*Percent*
29	9	0.426	21	0.5	0.4
32	69	.441	156	3.6	3.0
35	63	.411	153	3.3	2.9
38	97	.426	228	5.0	4.4
41	162	.368	440	8.4	8.5
44	250	.259	965	12.9	18.6
47	253	.254	996	13.1	19.2
50	284	.365	778	14.7	15.0
53	269	.490	549	13.9	10.6
56	231	.553	418	11.9	8.0
59	154	.554	278	8.0	5.4
62	61	.500	122	3.2	2.3
65	28	.385	78	1.4	1.4
68	4	.236	17	.2	.3
71	(2)	(.176)			

NOTE.—Length class 71 cm. was omitted.

1¼-inch gap between the 3¼- and 4½-inch mesh sizes. Both curves show peak catch efficiency at 56 cm. and 59 cm. The mode for sockeye is about 56 cm., for chum about 57 cm. The pink salmon curve shows peak catch efficiency at 53 cm. and lowest catch efficiency at 41 cm.

The shape of the catch efficiency curves for sockeye and chum salmon between 44 cm. and 62 cm. and for pink salmon between 38 cm. and 56 cm. is somewhat similar. The pink salmon curve is displaced to shorter fish. Pink salmon probably have greater girth per given length than the other two species, although no girth measurements of pink salmon were taken to verify this. Differences shown in figure 10 probably result from girth/length differences among the three species.

DISCUSSION

Certain assumptions in applying Holt's method were considered. One assumption was that standard deviations of selection curves should be similar. A computation of the S values for each year from 1956 to 1960 checked this assumption. Table 16 lists S values for each pair of mesh sizes. Sockeye and chum salmon S values are given for all years. Pink salmon S values were computed only for odd-numbered years; catches were small in even-numbered years.

Standard deviations of selection curves within each species were reasonably similar in at least the larger mesh sizes, 3¼-, 4½-, and 5¼-inch. Pink salmon had slightly higher S values and sockeye slightly lower S values in the paired 3¼- and 4½-inch mesh sizes than in the 4½- and 5¼-inch (table 16). Chum salmon also varied only slightly between these sizes. In the 2½- and 3¼-inch pair of mesh sizes, however, the S values for sockeye and chum salmon were low. The small 2½-inch mesh was probably the main cause of these low values.

TABLE 16.—*Standard deviation of mesh selection curves for pink, sockeye, and chum salmon by year*

Salmon species	Year	Standard deviation (paired mesh sizes)		
		2½-inch and 3¼-inch	3¼-inch and 4½-inch	4½-inch and 5¼-inch
		Centimeters	*Centimeters*	*Centimeters*
Pink	1957		5.4	4.6
Do	1959		4.9	4.4
Sockeye	1956	3.5	5.5	6.1
Do	1957	3.7	5.9	6.5
Do	1958	3.1	5.1	6.1
Do	1959	3.9	5.5	5.9
Do	1960	4.0	5.4	6.3
Chum	1956	3.6	5.6	5.3
Do	1957	3.4	5.6	6.5
Do	1958	3.7	4.4	5.5
Do	1959	3.6	5.0	5.4
Do	1960	3.8	5.2	5.1

Another assumption was that the mean selection length of salmon is proportional to mesh size. Mesh size (perimeter) is directly related to the fish's girth. Lander (1963) showed that the girth and length of sockeye and chum salmon of the high seas have a linear relation. Thus, the relation of length of salmon and mesh size warrants using proportionality constants (K values).

K values within species varied remarkably little annually (table 17). Between species, K values for pink salmon were lower than those for sockeye and chum salmon, probably because pink salmon have greater girth per given length. As shown in table 17, mean selection lengths had lower values in pink salmon than in the other two species.

All investigators did not use normal distribution for the mesh selection curve. Some used a skewed mesh selection curve, tailing off to the right, rather than a normal curve. Olsen (1959), working with Newfoundland herring data, found that logs of catch ratios followed a parabolic line better than a straight line. His selection curves, thus, are slightly skewed rather than normal. Ishida (1962) used a mesh-size ratio method in developing skewed selectivity curves for salmon from the North Pacific. Gulland and Harding (1961), using gill net catches of the African catfish *Clarias*, obtained a skewed selection curve with a long upper tail. The shape of *Clarias* (long fish with a large bony head) and the method of its capture (entanglement in

TABLE 17.—*Proportionality constants and mean selection lengths for pink, sockeye, and chum salmon*

Salmon species	Year	K[1]	Mean selection length by mesh size			
			2½-inch 6.35 cm.	3¼-inch 8.26 cm.	4½-inch 11.43 cm.	5¼-inch 13.34 cm.
			cm.	*cm.*	*cm.*	*cm.*
Pink	1957	4.28	27.2	35.4	48.9	57.1
Do	1959	4.21	26.7	34.8	48.1	56.2
		Mean	27.0	35.1	48.5	56.6
Sockeye	1956	4.53	28.8	37.4	51.8	60.4
Do	1957	4.62	29.3	38.2	52.8	61.6
Do	1958	4.49	28.5	37.1	51.3	59.9
Do	1959	4.62	29.3	38.2	52.8	61.6
Do	1960	4.60	29.2	38.0	52.6	61.4
		Mean	29.0	37.8	52.3	61.0
Chum	1956	4.63	29.4	38.2	52.9	61.8
Do	1957	4.68	29.7	38.7	53.5	62.4
Do	1958	4.68	29.7	38.7	53.5	62.4
Do	1959	4.67	29.7	38.6	53.4	62.3
Do	1960	4.73	30.0	39.1	54.1	63.1
		Mean	29.7	38.7	53.5	62.4

[1] K=Proportionality constant of fish length divided by mesh size.

several meshes) are thought to cause the asymmetry.

Other investigators besides Holt used normal distribution for mesh selection curves. McCombie and Fry (1960), working with Lake Huron whitefish data, concluded that normal distribution best describes the mesh selection curve. Using nylon gill net catches of *Tilapia* from Lake Victoria, East Africa, Garrod (1961) showed that normal distribution applies over most of the selection range of fish lengths but not at the extremes of this range. Garrod used the normal curve obtained from linear regression after discarding the extremes where the relation departs from linear. I also used the procedure of discarding the extremes and then applying the normal curve.

SUMMARY

1. A method for determining gill net selectivity described by Holt (1957) was applied to experimental gill net catches of pink, sockeye, and chum salmon from the high seas of the North Pacific Ocean and Bering Sea. This method develops mesh selection curves for gill nets of different mesh sizes from catch ratios at various fish lengths.

2. A normal mesh selection curve, representing relative catch efficiency of the mesh for different length classes of fish, was constructed for each mesh size, 2½-, 3¼-, 4½- and 5¼-inch, for each species. Normal distribution can be used validly when extreme sizes of fish caught by snagging and tangling rather than gilling are omitted.

3. A composite curve of relative catch efficiencies for combined mesh sizes shows that the four mesh sizes cover the range of salmon lengths. All length classes were not caught with equal efficiency. A lower catch efficiency at 44 cm. of 47 cm. for sockeye and chum salmon and 41 cm. for pink salmon, resulted from the larger (1¼-inch) gap between the 3¼- and 4½-inch mesh sizes. The gap between other adjacent mesh sizes was three-quarter inch.

4. The composite curve for each species was used to adjust gill net catches for selectivity effect. Adjustments were minor.

ACKNOWLEDGMENTS

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LIFE HISTORY OF THE GIZZARD SHAD, *DOROSOMA CEPEDIANUM* (LE SUEUR), IN WESTERN LAKE ERIE

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ABSTRACT

The rapid increase in the stocks of gizzard shad in Lake Erie since 1950 unquestionably had an important effect on the ecology of the lake. The present study, based on almost 24,000 fish collected by various means in 1952–55 in or near the island area of western Lake Erie was undertaken to provide information on the role of shad in the bionomics of the region.

The annulus of the gizzard shad scale is a valid year-mark. It is laid down in May–July, a little later in the older than in the younger fish. The body-scale relation is linear with an intercept of 22.1 mm. on the axis of standard length. Age-groups 0, I, and II were abundantly represented in the samples. Age-group III was was much less well represented, and older fish were extremely scarce. The oldest shad seen belonged to the VI-group.

The seasonal growth was most rapid in July–August and growth was much reduced or nil in January–April. Males attained the following average standard lengths (in millimeters) at the end of the indicated years of life: 1–141; 2–273; 3–313; 4–343; 5–349. For females these values were: 1–140; 2–285; 3–335; 4–364; 5–386.

The weight of the gizzard shad increased as the 3.07053 power of the length. The length-weight relation varied seasonally, annually, and, near the spawning season, according to sex and state of gonads.

Although the gizzard shad is distributed widely throughout the Mississippi Valley and in stream systems tributary to the Gulf of Mexico and the Atlantic Coast north to about lat. 40° N., some question exists as to whether it is native to the Great Lakes-St. Lawrence basin or has penetrated into this region in historic times. Gerking (1945) was of the opinion that this fish migrated from the Mississippi drainage into the glacial Great Lakes during the Lake Maumee outlet stage. Kirtland (1850) believed that it gained access to Lake Erie from the Mississippi drainage recently by way of various Ohio canal connections. Trautman (1957), on the other hand, thinks that the gizzard shad was present in Lake Erie waters before the advent of the canals. Miller (1957) believed the question of whether the shad is native to Lake Erie cannot be solved conclusively.

The establishment of gizzard shad in Lake Erie in large numbers appears to have taken place fairly recently, however, and their presence in Lakes Huron, Michigan, and Ontario became known subsequent to collections of the species along the south shore of Lake Erie. The report of gizzard shad in the St. Lawrence River at Quebec is of recent date. Fresh-water fishery investigations—especially of rough fish—were so meager prior to 1850 that shad could easily have been overlooked.

In the Great Lakes-St. Lawrence drainage the gizzard shad has been reported from Lake Michigan in the west to Quebec in the east, but it has become best established along the western and southern shores of Lake Erie and in streams tributary to these shores.

The role of the gizzard shad in the ecology of fish populations is difficult to assess. Its value as a link in the food chain is not to be questioned. On the other hand, no use for shad other than as forage fish has been developed and their rapid growth soon makes them too large for most predatory fish. Shad tend to overpopulate many waters to a degree that seems to be detrimental to other species. In some southern states reduction of numbers of shad is part of the fish-management program for certain waters.

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In the past years, the numbers of gizzard shad in Lake Erie were too few for the species to create any important problems, indeed, to have any real significance in the bionomics of the lake, but recently their abundance has increased enormously. Mass mortalities have created esthetic and public-health problems, water intakes have been plugged, and commercial fishermen have wasted hours sorting and discarding the worthless shad from their catches. From the fish-management standpoint, the question arises whether the value of shad as forage may not now be outweighed by their diversion of the productive capacity of the lake into commercially valueless fish. An inquiry into the natural history of the gizzard shad in Lake Erie, accordingly, has been much needed.

Only a few precocious male and female gizzard shad attain sexual maturity as age group I. Almost all males and a good percentage of females mature at age II and only rarely are III-group shad immature. Development of the egg and seasonal changes of the ovary are described. Egg production is highest in the II group—average of 378,990 per individual and 689 per gram of body weight. Spawning takes place from early June into July and is most intensive near mid-June. Heaviest spawning is at water temperatures of 67° F. or more. Early development to the attainment of the adult shape is described; particular attention is given to the development of the alimentary tract.

The anatomy of the digestive tract in the adult is described and comments are offered on the function of such organs as the pharyngeal pouches and the caeca. Tests were made for digestive enzymes in different parts of the tract. The gizzard shad is a filter feeder. Food varies widely with season and locality but consists mostly of phytoplankton and zooplankton.

The gizzard shad population has been increasing in Lake Erie. Commercial fishermen told me that 3 decades ago the "sawbelly" was something of a rarity—only an occasional one was caught. They have attained greatest abundance, according to these fishermen, since about 1950. Whether this increase results from adaptations to the Lake Erie environment, to changes in the character of the lake, or merely to increasing surpluses of shad beyond environmental and predatory inroads has not been determined.

Gizzard shad seem to be most plentiful in the shallow waters around the periphery of western Lake Erie, in the Bass Islands area, and especially in protected bays and mouths of tributaries. The numbers present here vary from season to season. They are most numerous in late summer and early fall when their abundance is increased by the recruitment of the young of the year. They are next most plentiful just prior to and during their spawning season in late spring when the mature shad congregate in the shallow waters. Then, too, in winter they concentrate in places into which warm streams flow. At other times they are rarely seen in numbers—frequently days go by without any captures of shad by the commercial fishermen of South Bass Island.

The tendency of shad to inhabit shallow water, their attraction in massive numbers to the warmer water of outlets from industrial plants and of inflowing streams, and the frequent mass mortalities doubtless have given rise to an exaggerated idea of their abundance. Nevertheless, they are plentiful and their numbers are growing. The shad problem is real in both a practical and a purely scientific sense.

MATERIALS AND METHODS

The investigation of the life history of the gizzard shad was based on almost 24,000 fish (about two-thirds of which were young of the year) captured in western Lake Erie and in streams tributary to the southwestern shore of this lake in 1952–55. Studies of age, length, weight, growth, reproduction, and fecundity were made for shad captured in the lake. Fish caught in Sandusky Bay and in the tributary streams were omitted from those phases of the study because of differences in growth and other aspects of their life history.

The Sandusky Bay specimens were decidedly smaller than lake fish of the same age and appeared to have formed their annuli earlier in the year. Also, they probably spawned earlier than the lake-dwelling gizzard shad. The water in Sandusky Bay was frequently turbid—the shallow water is readily turned over by winds. Phytoplankton, though reduced by this turbidity, is not lacking, for much is washed into the bay from the marshes by the tributary streams. Stomach contents of fish caught in Sandusky Bay were largely muddy. The slower growth of the fish here probably

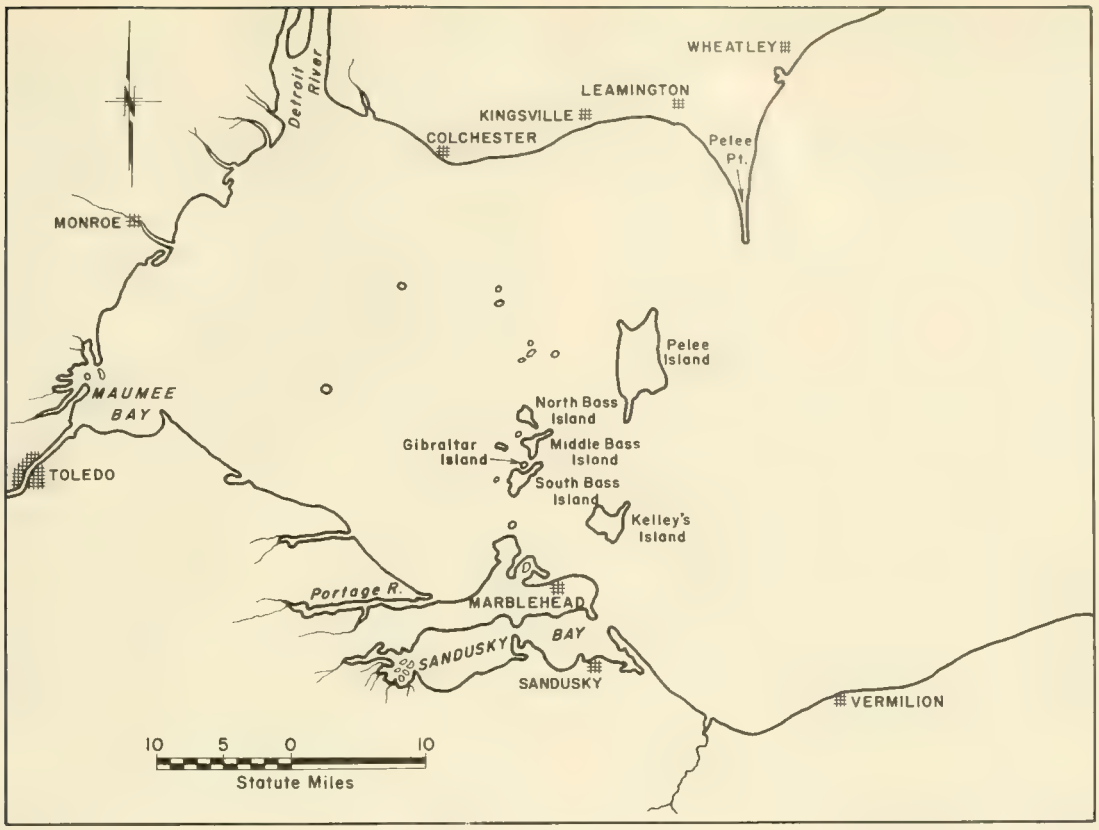

FIGURE 1.—Western Lake Erie where gizzard shad were collected in 1952–55.

resulted from the reduced nutriment. The earlier annulus formation and spawning are undoubtedly related to the earlier warming of the shallow waters in the bay.

The gizzard shad caught in the streams were not as deep-bodied as either the lake or the Sandusky Bay fish; and they were smaller, age for age, than those captured in Sandusky Bay. They were thinner, more gracefully shaped individuals, seemingly better adapted for swimming in streams. Probably the colder water and the poorer food supply were responsible for their slower growth.

Methods, Dates, and Sites of Collection

With the exception of gizzard shad from Sandusky Bay or tributary streams and a few otter trawl collections in the open lake, all samples were captured in western Lake Erie within one-half of a mile of island or mainland shores (fig. 1).

Gizzard shad were captured in the deeper water by 5-inch mesh (stretched measure) gill nets and standard commercial trap nets. Closer to shore, in 4 to 10 feet of water, I collected them by means of 4-inch mesh gill nets, experimental gill nets with meshes ranging from 1 to 4 inches, dynamite, rotenone, and electric shocks. In waters less than 4 feet deep, along the shore, I used "Common Sense" seines, a push seine, bag seine, and dip net. In Sandusky Bay the fishermen employed haul seines. See table 1 for methods of collection for each month and year and table 2 for methods of collection for each locality.

Data Recorded for Individual Fish

All fish lengths in this paper are standard lengths, in millimeters. Lengths of small fish were determined with the aid of a pair of dividers. Larger fish were measured on a measuring board. Most of the measurements were taken shortly after the fish were caught. When the sample was large, some of the fish were kept temporarily (1 to 2 days) in 10 percent formalin. Preservation in formalin for a week resulted in no perceptible

TABLE 1.—*Number of gizzard shad collected in 1952–55 by methods, year, and month*

[Number of samples in parentheses]

Year and month	Method of collection										Total
	Small-mesh seine[1]	Haul seine	Picked up dead	Experimental gill net	4- or 5-inch mesh gill net	Commercial trap net	Otter trawl	Dynamite	Rotenone	Electric shocking	
1952:											
July	125 (5)										125 (5)
Aug.	27 (3)				247 (1)						274 (4)
Sept.	9 (2)					17 (2)					26 (4)
Oct.	1 (1)										1 (1)
Nov.	183 (7)					77 (1)					260 (8)
Dec.	92 (6)						390 (2)				482 (8)
1953:											
Jan.	24 (3)						7 (1)				31 (4)
Feb.			27 (5)								27 (5)
Mar.			2 (1)								2 (1)
Apr.					1 (1)	324 (17)					325 (18)
May		115 (1)				129 (6)					244 (7)
June	81 (3)	158 (2)									239 (5)
July	1,456 (11)	64 (3)									1,520 (14)
Aug.	836 (10)	34 (4)		543 (2)						67 (3)	1,480 (19)
Sept.	26 (2)					1,195 (6)					1,221 (8)
Oct.	4 (1)			158 (2)		725 (10)					897 (13)
Nov.					13 (4)	1,762 (9)					1,775 (13)
Dec.					21 (6)	403 (1)	2 (1)				426 (8)
1954:											
Jan.			63 (1)		46 (9)						109 (10)
Feb.			44 (1)		242 (16)						286 (17)
Mar.					20 (7)						20 (7)
Apr.					29 (8)	39 (8)					68 (16)
May					18 (7)	63 (11)					81 (18)
June	268 (2)				427 (21)	713 (14)					1,408 (37)
July	143 (9)				227 (8)	540 (16)			650 (2)		1,560 (35)
Aug.				94 (2)	120 (7)	77 (2)		7,428 (2)	943 (2)		8,662 (15)
Sept.								876 (1)			876 (1)
Oct.				132 (1)							132 (1)
Nov.											
Dec.											
1955:											
Jan.					3 (1)						3 (1)
Feb.					19 (8)						19 (8)
Mar.					2 (1)	2 (1)					4 (2)
Apr.					161 (5)	148 (9)					309 (14)
May					6 (3)	204 (12)					210 (15)
June					459 (44)	284 (6)					743 (50)
Total	3,275 (65)	371 (10)	136 (8)	927 (7)	2,061 (157)	6,702 (131)	399 (4)	8,304 (3)	1,593 (4)	67 (3)	23,835 (392)

[1] Of various types mentioned in text.

TABLE 2.—*Gizzard shad collected in 1952–55 by method and locality*

[Number of samples in parentheses]

Locality	Method of collection										Total
	Small-mesh seine[1]	Haul seine	Picked up dead	Experimental gill net	4- or 5-inch-mesh gill net	Commercial trap net	Otter trawl	Dynamite	Rotenone	Electric shocking	
Fishery Bay (South Bass Island, Ohio)	2,350 (38)		126 (7)	927 (7)	1,558 (134)			8,304 (3)	1,593 (4)	67 (3)	14,925 (196)
Bass Islands, Ohio (except Fishery Bay)	27 (1)				316 (21)	6,702 (131)	399 (4)				7,444 (157)
Sandusky Bay, Ohio	76 (4)	371 (10)									447 (14)
Portage River, Ohio	116 (7)										116 (7)
Sandusky River, Ohio	233 (4)										233 (4)
Kelleys Island, Ohio	28 (2)										28 (2)
Pelee Island, Ontario	218 (2)										218 (2)
Green Creek Marsh, Ohio	46 (1)										46 (1)
East Harbor, Ohio	74 (1)										74 (1)
Colchester, Ontario	26 (1)										26 (1)
Long Point, Mich.	44 (1)										44 (1)
Point Pelee, Ontario	10 (1)										10 (1)
Avon Lake, Ohio					187 (2)						187 (2)
Mouse Island, Ohio	4 (1)										4 (1)
Maumee Bay, Ohio	23 (1)										23 (1)
Vermilion, Ohio			10 (1)								10 (1)
Total	3,275 (65)	371 (10)	136 (8)	927 (7)	2,061 (157)	6,702 (131)	399 (4)	8,304 (3)	1,593 (4)	67 (3)	23,835 (392)

[1] Of various types mentioned in text.

change in length; and the loss in weight was about 1 percent.

The relation of total length to standard length was obtained by fitting a line by means of least squares to the length measurements. The regression equation was $L_t=4.9+1.23\ L_s$, where L_t is total length and L_s is standard length.

For the determination of age, three or more scales were removed from every gizzard shad longer than 100 mm. Among the smaller shad, scales were taken from random samples of fish from each collection. The scales were placed on a glass slide immediately after removal from the fish, and their annuli counted with the aid of a dissecting microscope. The ages assigned were in terms of the number of annuli. Since the age designation changes on January 1, a fish captured between this date and the actual time of annulus formation was credited with a "virtual annulus" at the edge of the scale (Hile, 1948).

The scales employed in the study of the body-scale relation and for the calculation of growth were removed from a "key area." Since gizzard shad lose their scales readily, a "key scale" frequently would have been missing or regenerated. Use of a key area eliminated discarding shad which lacked the one particular key scale. The key area is on the left side of the fish, just dorsal to a midlateral line and midway between the posterior edge of the operculum and the origin of the dorsal fin. A dozen or so scales from this area were placed in a scale envelope on which was recorded the information pertinent to the fish.

Three nonregenerated scales were taken at random from these key-area scales. For study, they were either impressed on strips of plastic by a cold roller press (Smith, 1954) or mounted dry on glass slides.

The scale measurements were obtained from scale images projected by a microprojection apparatus of the type described by Van Oosten, Deason, and Jobes (1934).

Computations of growth from scale measurements were made nomographically.

Weights are expressed in grams. The largest fish were measured to the nearest gram, fish between 100 and 200 mm. in standard length to the nearest 0.5 g. and those smaller than 100 mm. to the nearest 0.1 g. In catches of large numbers of gizzard shad smaller than 50 mm., those of equal length were weighed en masse and the average weight assigned to each member. Fish preserved for a few days in formalin were sometimes used. Some fish were not weighed when collections were large. Gonads -only from freshly caught shad - were weighed to the nearest 0.01 g.

Ovaries from potential spawners caught in May, June, and July were used for egg counts. From one of the weighed ovaries a small transverse section (1 to 2 g.) was removed and weighed on an analytical balance, its content of current-season eggs counted, and the number of eggs in the entire ovary calculated.

Histological preparations were made of the ovaries of some fish captured in different seasons for studies of oögenesis and ovarian growth and development.

Sex was always determined by dissection except for those fish from which eggs or milt were flowing during the spawning season. When possible, sex was determined for all fish longer than 120 mm. Maturity of males could not be determined in the absence of flowing milt.

SCALE OF THE GIZZARD SHAD

Description of the Scale

The gizzard shad has cycloid scales whose annual growth zones contain many circuli. The relatively closer juxtaposition of the circuli in the first growth zone than in the succeeding zones contributes a darker appearance to this inner portion of the scale. The closely set circuli of this zone are gently arched and, save for those formed earliest, do not curve enough at their ends to reach the transverse groove that separates the anterior and posterior fields but terminate in the lateral fields. This pattern is followed by the circuli of each succeeding growth zone; i.e., the earliest circuli reach the transverse groove, while those produced later terminate laterally. The first circulus of the second growth zone is closely juxtaposed to the last circulus of the preceding zone in the anterior field, cuts across the paths of the later first-zone circuli at their terminations in the lateral fields, and intersects the transverse groove. Thus, it forms roughly a semicircle around the first growth zone. The junction between the first and second growth zones (fig. 2) illustrates one type of demarcation line in the gizzard shad scale. The first annulus of all shad scales examined was of this type. Since this annulus normally is evident only in the lateral

fields where the termination of the circuli of the first zone is "cut across" by the circuli of the second zone, it may escape notice under low magnification.

A second type of demarcation line, characterized by a narrow band devoid of clear-cut circuli, normally is found between all growth zones beyond the first. Here, too, the earlier circuli of the more recent zone cut across the paths of the later circuli of the preceding zone in the lateral fields. This type of annulus is clearly evident under low magnification (fig. 3).

Further study is required, but on the basis of my observations I suggest that this second type of annulus is a combination spawning mark and annulus. It is found only on the scales of fish of spawning age. The prominence of this annulus and its possession of a few fragmentary circuli indicate not only a cessation and resumption of growth, but also a period of either poor circulus formation or even of limited scale resorption. Such a period is not indicated by the first annulus. Annulus formation and spawning take place at about the same time (see next section on time of annulus formation). Although no direct causative relation between spawning and annulus formation has been demonstrated, the period of disturbed circulus formation may well be the result of rapid prespawning gonad growth. A few gizzard shad do not spawn during their third year of life (near the start of which the second annulus is formed). These fish may provide the scales on which the second annulus resembles the normal first annulus closely. This type of annulus (fig. 4) lacks the narrow band of fragmentary circuli which makes the usual second and succeeding annuli so conspicuous.

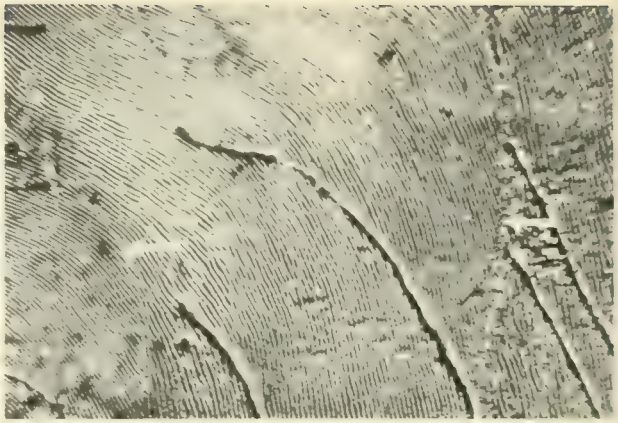

FIGURE 4.—Second annulus of a gizzard shad scale resembling typical first annulus.

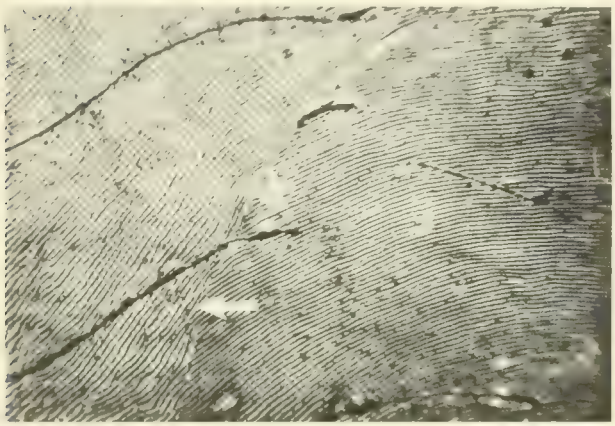

FIGURE 2.—The first annulus of a gizzard shad scale.

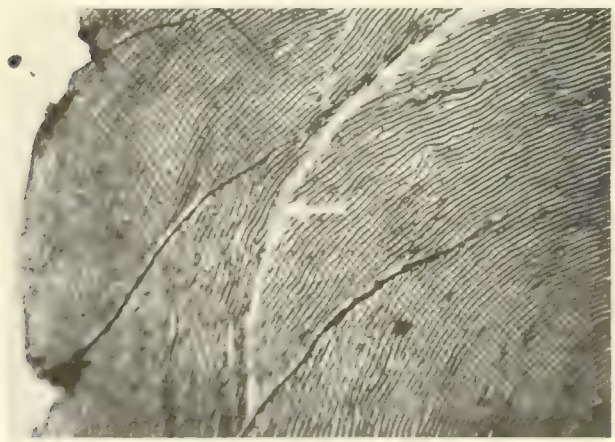

FIGURE 3.—The second annulus of a gizzard shad scale, with clear line between second and third growth zones.

Further evidence on the possible effect of spawning on scale structure comes from gizzard shad that show an accessory check between the first and second annuli of their scales (fig. 5); in fact, all accessory checks found were in this position. Fish with this check may be the few shad which spawn during their second year of life. Because the first annulus is already present by the first of June, whereas any precocious second-year spawning occurs in late July—or later in the year (see section on spawning season)—the effect of this late spawning, if it is to be shown by the scale, would have to appear beyond the first annulus.

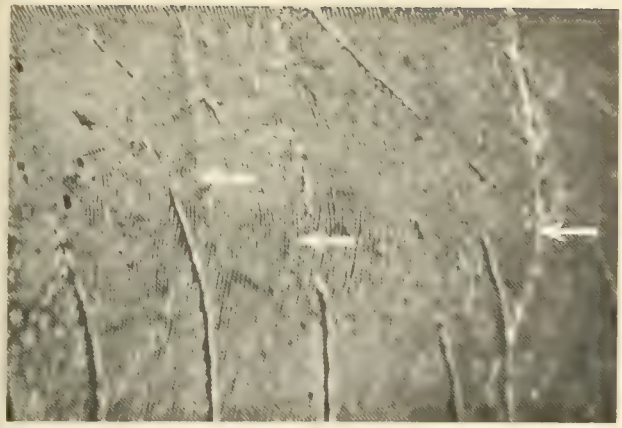

FIGURE 5.—An accessory check on a gizzard shad scale.

Time of Annulus Formation

No new annuli were observed on the scales of any age group of gizzard shad collected in the lake prior to the second quarter of May (table 3). Data for individual days in this second quarter indicated that two of the five males and eight of the nine females of age-group I, taken in the open lake on May 15, had already formed their first annulus. Only one other of the I-group fish, a female captured on May 12, 1955, collected in this quarter had the new annulus. No fish of this age group exhibited annuli in the small collections of May 16–23. (All of the 48 male and 56 female I-group fish caught in Sandusky Bay on May 22, 1953, had their new annulus—data not given in table.) All I-group shad collected after May, however, had completed the new annulus. The new annulus of the II-group fish began to appear in the first quarter of June and the year-mark was present in all of these fish by the first quarter of July. Shad older than the II-group seem to have formed the new annulus about a week later; data for these higher ages, however, are meager. The time of annulus formation, as judged from examination of scales, is in general agreement with the time of resumption of growth in length as indicated by changes in the length of fish (see fig. 8).

Once annulus formation had started, the percentage of females having the new annulus was greater than that of the males until all fish of both sexes had new annuli. On the whole, the female gizzard shad seems to form the annulus as much as a week earlier than the male.

Among the II-group shad, neither length nor weight of either sex was a determining factor in time of annulus formation (a similar study was not made of other age groups). A comparison (made only for June) of the II-group female gizzard shad which had not spawned with those which were spent demonstrated that the percentage of fish having the new annulus was about the same in both groups. Hence, we may assume that the act of spawning neither hastened nor retarded the formation of the new annulus. It may not be concluded, however, that the gonad development which ultimately results in spawning has no effect on the structural appearance of the developing annulus or upon the initiation of a check. Probable evidence of the effect of spawning is seen in the accessory check found between the first and second annuli in the scales of some shad (see previous section on description of the scale).

Validity of the Annulus as a Year-Mark

Lagler and Applegate (1943) and Lagler and Van Meter (1950) demonstrated that the annulus is a true year-mark on scales of gizzard shad in Indiana and Illinois. The following data on shad in Lake Erie add support to the belief that annuli

TABLE 3.—*Percentage of gizzard shad having a new annulus in May, June, and July*

[Combined collections of 1953–55; lake specimens only. Number of fish in parentheses]

Age and sex	Periods in May				Periods in June				Periods in July			
	1–8	9–15	16–23	24–31	1–8	9–15	16–23	24–30	1–8	9–15	16–23	24–31
I-group:												
Male	0.0 (51)	9.1 (22)	0.0 (4)	. . .	100.0 (10)	. . . .	100.0 (83)	100.0 (18)	100.0 (50)	100.0 (1)	100.0 (55)	100.0 (21)
Female	.0 (74)	23.7 (38)	.0 (1)		100.0 (8)	. . . .	100.0 (37)	100.0 (19)	100.0 (75)	100.0 (3)	100.0 (71)	100.0 (20)
II-group:												
Male	.0 (23)	.0 (37)	.0 (23)	0.0 (4)	24.2 (120)	8.4 (166)	52.0 (246)	84.9 (86)	100.0 (29)	100.0 (7)	100.0 (27)	100.0 (2)
Female	.0 (34)	.0 (48)	.0 (37)	. . .	32.8 (67)	30.7 (75)	66.4 (125)	96.9 (97)	100.0 (47)	100.0 (13)	100.0 (16)	100.0 (5)
III–VI-group:												
Male	.0 (3)	. . . . .	.0 (6)	.0 (1)	.0 (16)	.0 (26)	.0 (24)	50.0 (2)	75.0 (4)	100.0 (1)	.0 (1)	. .
Female	.0 (3)	.0 (5)	.0 (4)	.	.0 (5)	.0 (8)	16.1 (31	75.0 (32)	100.0 (26)	95.2 (21)	. . .	.

are valid indicators of age. (Later sections include considerable supporting data on certain of the points.)

1. Gizzard shad known to be young of the year had no annuli on their scales.

2. The scales of these young shad captured in the fall, winter, and early spring showed no annulus at the edge, whereas those taken later exhibited increasing percentages with an annulus until all possessed them.

3. The distance between the last annulus and the scale edge increased through the growing season.

4. Presumed age groups as indicated by modes in length-frequency groupings of shad agreed with groupings based on the number of annuli.

5. The calculated lengths for particular years of life among the age groups of the same and different years of collection agreed with estimates of length from modes of frequency distribution.

Body-Scale Relation

The relation between fish length and scale length in gizzard shad was determined from the "key-area" scales of some 700 fish, ranging in standard length from 43 to 390 mm. A test plotting of the length of the anterior radius (center of focus to anterior edge) of the scale against the standard length of the fish indicated the relation to be linear. The regression line, $L=22.1+44.25\ S$, was fitted by least squares; L=standard length of the fish in mm. and S=anterior radius of the scale in mm. Fish captured in every month and including age-groups I through VI of both sexes are represented in this equation. Studies of the body-scale relation for each sex, for each age group, and during each month revealed no appreciable variation from the general equation.

The empirically derived body-scale equation was the basis for construction of a nomograph for the calculation of growth from scale measurements.

AGE COMPOSITION

Seasonal movements, segregation by size and possibly by maturity, and selectivity of collecting methods complicated the problem of sampling for age composition. The very young gizzard shad of western Lake Erie were found in midsummer close to shore, usually in shallow water. Collecting representative samples of these fish presented difficulties. Capture of the very youngest required the use of dip nets which, of course, the larger fish eluded. As the season progressed and the fish grew larger, Common Sense seines and bag seines were used, but this gear permitted the very smallest fish to pass through the meshes while many of the larger ones escaped capture by their agility and speed. The use of rotenone was selective for the very young shad that could not swim through the poisoned water rapidly enough to avoid being overcome. (Rotenone was used in small areas in the lake with no provisions for holding the fish within the sampling area or for preventing dissipation of the poison into the surrounding waters.) Electrocuting, on the other hand, was selective for the larger shad—the very young ones were unaffected. Finally, I used dynamite. This method proved most successful because fish of all sizes and ages surfaced within the radius of its effectiveness.

As the young gizzard shad become larger (and older) they move into deeper water offshore. By October, the Common Sense seine, which must be fished inshore, will capture some O-group shad but no I-group or older ones; hence, its catches yielded no data on age composition. The gill net captures large O-group shad and also all the older age groups in October, but many smaller O-group shad must pass through the net. Because of these sampling problems, estimates of age composition are unreliable among the 4- to 8-inch shad. Only a few fish of these sizes were captured by experimental gill nets whose meshes ranged from 1 to 4 inches, stretched measure.

Except during the spawning season, gizzard shad older than age-group III were rarely found in the shallower waters. This preference for the deeper water seemed to increase with age.

In view of the segregation by size and the seasonal changes of distribution, small-scale methods of collection could not provide suitably accurate data on age composition. I lacked especially the means to compare data on the 1- to 4-inch group from the shallow waters with records for larger shad from the deeper waters.

Seasonal Changes of Age Composition

Because of the difficulties just outlined, O-group gizzard shad caught by any means other than by trap nets and 4-inch-mesh gill nets have been excluded from this section. The O-group shad

in our collection area appear in June, rise to greatest abundance about late July, and diminish in numbers thereafter. Greatest losses occur, presumably, as a result of predation and migration from the collection area.

Although O-group gizzard shad were taken in greatest numbers in late July, none of them had become large enough to be caught by the gill nets and trap nets until August. Subsequently, the size of the collections of the O-group coming into this catchable size range increased regularly until they reached peak abundance toward the end of the calendar year (table 4). They were the dominant age group among fish taken by these nets from August to the end of the year. From January to August of the next year, contrary to expectation, these fish, as the I group, were not dominant in the catch of gill nets and trap nets. Over this period the II-group fish dominated the catches. After August, however, the I group became more plentiful than the older groups and maintained that abundance thereafter.

The scarcity of I-group gizzard shad in the gill net and trap net samples from January to August cannot be fully explained. When all the fish captured in January–July are considered (whether they were obtained by dynamite, rotenone, electrocution—data not tabulated here), then the I group is the dominant group in the collecting area in all the early months except June and July. The June collection especially is noteworthy—the I group was very poorly represented in samples from both the lake and Fishery Bay—especially in the bay where only 4 I-group shad were collected along with 820 II-group fish.

It is noteworthy that the II-group and older shad were taken principally in April through July. Only during the spawning season (June–July) was I able to capture the VI-group shad, which were the oldest in the samples. The August–September samples were dominated overwhelmingly by age group I (89.0 to 98.8 percent). The II group made up 1.2 to 10.6 percent, and only four older fish were taken in the 5 months.

Sampling difficulties, as previously described, prohibited any detailed consideration of fluctuations of year-class strength; however, the 1952 year class apparently was one of unusual abundance. In random samples from commercial trap nets this year class made up 85 percent of the total as age group I, 71 percent as age group II, and 11 percent as age group III.

TABLE 4.—*Age composition of gizzard shad taken by trap nets and 4-inch-mesh gill nets, Lake Erie, 1954*

[Percentages of fish in age-groups I–VI given in parentheses—the O-group fish were not considered in the computation of percentages or average age]

Month	Age group							Total and average age [1]
	O	I	II	III	IV	V	VI	
Jan.	(2)	4	44	1				49
		(8.2)	(89.8)	(2.0)				1.94
Feb.	(2)	12	56	3	2			73
		(16.5)	(76.7)	(4.1)	(2.7)			1.93
Mar.	(2)	2	16	5				23
		(8.7)	(69.6)	(21.7)				2.13
Apr.	(2)	316	330	36	7	1		690
		(45.8)	(47.8)	(5.2)	(1.0)	(0.1)		1.62
May	(2)	190	187	16	5	1		399
		(47.6)	(46.9)	(4.0)	(1.3)	(.3)		1.60
June	(2)	44	1,656	125	14	2	2	1,843
		(2.4)	(89.9)	(6.8)	(0.8)	(.1)	(0.1)	2.07
July	(2)	287	446	29	4	1	1	768
		(37.4)	(58.1)	(3.8)	(.5)	(.1)	(.1)	1.68
Aug.	256	226	27	1				254
		(89.0)	(10.6)	(0.4)				1.11
Sept.	899	304	7	1	1			313
		(97.0)	(2.2)	(.4)	(.4)			1.04
Oct.	667	221	15	1				237
		(93.2)	(6.3)	(.5)				1.07
Nov.	1,686	164	2					166
		(98.8)	(1.2)					1.01
Dec.	320	97	5					102
		(95.1)	(4.9)					1.05

[1] Average number of annuli.
[2] Young of the year first became available to the nets in August.

Survival Rate

Although the records (table 4) do not give a fully satisfactory idea of the age composition of the gizzard shad stock, the collections made in April–July probably permit fairly reliable inference as to the ratios between the numbers in successive age groups for II-group and older shad, since these mature fish seem to constitute a homogeneous group during this period. Collections made from August to December are probably reasonably reliable for determining the ratio of the I-group to the II-group shad. From these two sets of data, I have estimated the survival rate of shad from one age group to the next higher one (table 5).

An estimate (not given in table 5) was made also of the survival of gizzard shad from egg deposition to age-group I. The first step was the calculation, from data on sex ratio (table 15) and fecundity (table 18), of the probable number of eggs deposited by the gizzard shad of age-group II and older. The females of the 6,049 fish (total of the II-group and older of the right-hand column of table 5) were thus estimated to have deposited 926 million eggs. If the 100,000 I-group fish of table 5 are held to be the survivors of this number of eggs (it is assumed that the population is relatively

stable), survival from the egg to age-group I is determined as 0.011 percent. This estimate is beset with many uncertainties. It assumes, for example, that the determination of the number of I-group individuals from the ratio of numbers of fish in age-groups I and II in August–November samples was accurate; that year-to-year differences of stock were small enough to justify the pooling of data in the preparation of table 4; that the samples that contributed to table 5 were not unduly biased by gear selection or segregation by size or sex. Even if we granted the survival of 0.011 percent from egg to I-group a wide margin of error, however, the extremely low value still indicates an enormous mortality.

The extraordinarily low survival of the gizzard shad from eggs to the I-group fish probably results from heavy egg and larval mortality, predation, and (in late fall and early winter) buffeting during storms as well as rapid variations in water temperature. When they become the I-group fish, they are usually too large to be eaten by most predatory fish, but they are susceptible to storms and temperature changes that are greatest in waters relatively close to shore where this age group is usually found. As the shad become older, the survival rates improve, probably because the fish tend to remain in the deeper waters where they are less subjected to climatic disturbances.

The oldest gizzard shad that I collected from the western end of Lake Erie in 1952–55 were three of age-group VI (seventh year of life). Patriarche (1953) reported X-group gizzard shad from Lake Wappapello, Mo.

TABLE 5.—*Survival of gizzard shad from one age group to the next higher one*

[The figures in the first column, body of table, obtained from table 4]

Period of capture and age group	Number of fish	Survivors from 100,000 I group
August–December		
I	1,012	100,000
II	56	5,534
April–July		
II	2,619	5,534
III	206	435
IV	30	63
V	5	11
VI	3	6

LENGTH-WEIGHT RELATION

General Relation

The mathematical relation between length and weight of gizzard shad captured in western Lake Erie in 1952–55 was determined by fitting the equation $W=cL^n$ to the average empirical lengths and weights of fish in each 10-mm. length interval. The length-weight relation was investigated for each month in which sufficiently large samples were taken. Between mid-1952 and mid-1955 there were 25 such monthly samples. At least one equation was determined for each of the 12 months (for some months adequate samples were acquired in each of the 2 or 3 years—hence, two or three equations). For a month having more than one equation, length and weight data were obtained by each equation, and from these an average monthly length-weight relation was determined. In like manner a "general" length-weight equation was determined from the data calculated by the monthly equations. The sexes were combined for all monthly equations. The general equation was $\log W=-4.81765+3.07053 \log L$, where W is the weight in grams and L is the standard length in millimeters.

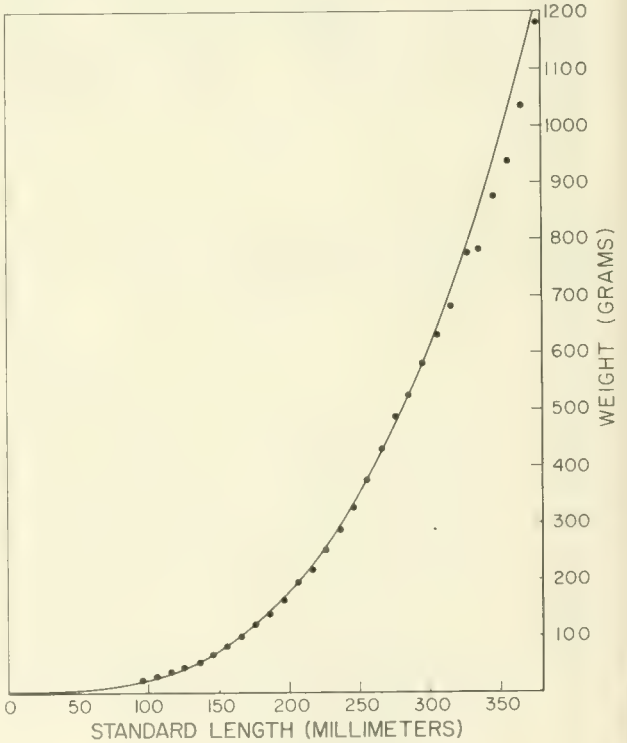

FIGURE 6.—Length-weight relation of gizzard shad in western Lake Erie. The curve is a graph of the general length-weight equation; the data represent the mean empirical values, derived as explained in the text, for the combined collections of 1952–55.

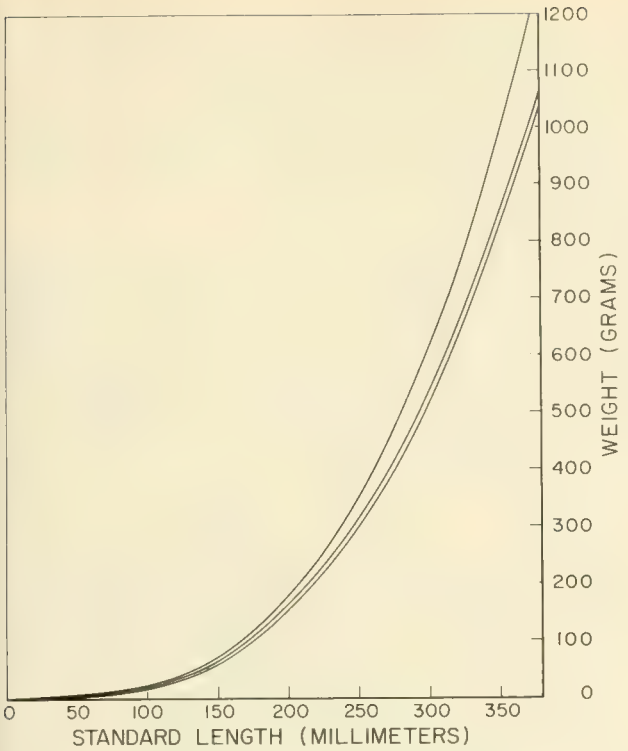

FIGURE 7.—Length-weight curves for gizzard shad from Lake Erie, Missouri, and Illinois. Left curve, Lake Erie; middle curve, Missouri; right curve, Illinois.

Empirical weights and the weights calculated by the general length-weight equation (table 6; fig. 6) agreed well in view of the heterogeneous nature of the materials (records of weight were combined without regard to season, year, sex, maturity, or method of capture). Largest disagreements in measurements concerned the longest fish.

Patriarche and Lowry (1953) determined the length-weight equation to be log $W = -2.2071 + 2.9812 \log L$ for gizzard shad in the Black River Basin of Missouri. Lagler and Van Meter (1950) reported the equation to be log $W = -2.2789 + 3.034 \log L$ for shad in Illinois. In both equations, the units are weight in ounces and total length in inches. The curves based on these equations show the Lake Erie shad to be heavier for corresponding lengths than those in Missouri and Illinois (fig. 7).

The weights of male and female gizzard shad were closely similar except in June and July, when the females were consistently heavier than males of corresponding length. This difference frequently has been explained on the basis that

TABLE 6.—*Empirical weights and weights calculated by the general length-weight equation for gizzard shad in western Lake Erie, 1952–55*

Standard length	Weight		Standard length	Weight	
	Empirical	Calculated		Empirical	Calculated
Millimeters	*Grams*	*Grams*	*Millimeters*	*Grams*	*Grams*
20	0.08	0.15	226	251	257
30	.5	.5	236	289	295
40	1.3	1.3	246	328	333
96	20	19	256	373	376
106	26	25	266	428	424
116	35	33	276	484	473
125	43	42	285	525	526
136	54	54	295	581	583
146	67	67	305	629	645
156	82	82	315	680	713
166	99	99	326	776	794
176	118	119	335	781	864
186	138	141	344	876	938
196	161	165	355	937	1,032
206	194	193	365	1,034	1,118
215	215	222	377	1,179	1,234

the female's ovaries are heavy with eggs soon to be spawned. Although the weight of the ovaries contributes strongly to the heavier total weight of the female gizzard shad, it does not explain it entirely. To investigate this point, the body weight (exclusive of gonad weight) of both sexes should be compared. Unfortunately, I had taken relatively few gonad weights of males—and these over a period of several months which cut across the seasonal changes of weight. However, since the testis weight averaged 1.4 percent of the body weight for these males, I thought I could eliminate the greater part of the weight advantage offered by the ovary by adjusting the female shad's weight to include ovaries weighing only 1 percent of her body weight.

The adjusted weights of these fish were still greater than those of male shad of corresponding length (table 7). The lesser weight of males may result from their greater activity during the spawning season.

Effect of State of Ovaries on Weight

The study of the effect of the state of development of the ovaries on the weight of the fish was based on records for three categories of fish caught in June 1955: will not spawn, will spawn, and spent.

The gizzard shad that would not have spawned were the heaviest (table 8). The average weight of females which would have spawned was 96 percent of that of the shad which would not have spawned. It appears that the production of mature eggs for spawning reduces the fish's total weight—possibly because some food is stored as

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TABLE 7.—*Comparison of weights of male shad at 20-mm. intervals with those of females whose weights have been adjusted to include ovaries of only 1 percent of their body weight*

[Based on June 1955 collection]

Standard length	Weight	
	Males	Females
Millimeters	*Grams*	*Grams*
200	158	189
220	210	244
240	271	309
260	344	383
280	428	467
300	525	563
320	636	669
340	760	788
360	900	919

oil in the eggs rather than as the heavier protein of flesh. The spent fish weighed the least. Their average weight was 85 percent of that of the fish which would not have spawned during the current season. The average percentage loss of weight of mature females at spawning increased with length of fish and averaged 10.7 percent.

Seasonal Differences in the Weight of Fish of a Given Length

The weight of gizzard shad of a given length varies from season to season, and this seasonal variation is similar from year to year. The nature of the seasonal changes (table 9) appears from the average monthly length-weight data. In June and July, when weights of the sexes differed appreciably, the males and females were treated both separately and combined; in other months they were combined.

Gizzard shad attained their greatest weight in August–October, after which the weight declined slowly and irregularly, reaching a low for the combined sexes about May–June. (Interpretations are handicapped by differences of slope in the monthly logarithmic lines.) During the next 2 months, the weights increased rapidly. The weight of the female was least in May (not shown in table 9), and an increase was obvious in June, but that of the male reached the lowest point in June.

Studies of the gut contents indicate that gizzard shad consume little food in winter and early spring. During this period they subsist largely on energy stored in the body tissues. Because metabolic rates are low in winter, decrease of the body weight is slight. As the water temperature rises in early spring, the metabolic rate of the fish increases more rapidly than the rate of food intake and the body weight decreases more rapidly. This process gains momentum with the progression of spring until about May–June when the lowest body weight is attained apparently just before the renewed feeding begins to meet the energy requirements of the fish. The occurrence of peak weight, in August–October, undoubtedly is directly related to feeding.

Continued loss of weight in June among the males can be attributed to their spawning activities.

TABLE 8.—*Weights of three groupings of female gizzard shad of different ovarian development, June 1955*

Standard length	Weight of females in category			Loss at spawning
	Would not have spawned	Would have spawned	Spent	
Millimeters	*Grams*	*Grams*	*Grams*	*Percent*
280	510	484	473	2.3
300	610	583	543	6.9
320	722	694	617	11.1
340	846	818	695	15.0
360	982	954	779	18.3

TABLE 9.—*Monthly variations of weight of gizzard shad as determined from the monthly length-weight equations*

WEIGHT

Standard length	January	February	March	April	May	June			July			August	September	October	November	December
						Males	Females	Combined sexes	Males	Females	Combined sexes					
Millimeters	*Grams*	*Grams*	*Grams*	*Grams*	*Grams*	*Grams*	*Grams*	*Grams*	*Grams*	*Grams*	*Grams*	*Grams*	*Grams*	*Grams*	*Grams*	*Grams*
200	177	170	179	157	158	161	192	177	186	183	185	198	193	189	181	183
220	240	228	240	215	212	213	249	231	241	242	242	264	256	256	241	245
240	317	298	314	287	277	275	315	295	304	313	309	342	330	336	313	320
260	410	381	402	374	355	348	391	370	377	397	387	435	419	433	398	409
280	519	479	506	478	446	433	478	455	460	494	478	543	521	547	497	514
300	646	593	626	600	551	531	575	553	553	606	580	668	639	680	612	635
320	794	723	764	743	673	642	685	663	658	734	696	810	773	834	742	774
340	963	872	922	907	811	767	807	787	774	878	826	972	924	1,010	890	933
360	1,156	1,039	1,100	1,096	967	908	942	924	902	1,040	971	1,153	1,094	1,209	1,056	1,111

TABLE 10.—*Annual differences of weights of gizzard shad in 1952–55*

[Years compared by pairs; data limited to months for which records are available for both members of the pair]

Standard length	Weights by years									
	1952	1953	1952	1954	1953	1954	1953	1955	1954	1955
Millimeters	*Grams*	*Grams*	*Grams*	*Grams*	*Grams*	*Grams*	*Grams*	*Grams*	*Grams*	*Grams*
200	190	186	197	189	172	174	154	169	165	172
220	253	249	264	252	231	237	207	226	223	229
240	330	326	345	326	303	312	272	296	293	297
260	421	416	442	415	389	403	348	379	378	378
280	525	523	555	517	490	510	440	476	478	472
300	650	645	686	636	608	636	546	590	595	581
320	790	787	837	771	744	781	668	720	730	705
340	950	948	1,008	924	898	948	807	869	885	846
360	1,146	1,130	1,204	1,096	1,078	1,138	966	1,036	1,061	1,005
Rating of years	1952>1953		1952>1954		1953<1954		1953<1955		1954>1955	
Months used	Aug., Nov., Dec.		Aug.		Jan., Feb., Apr., May, Aug., Oct.		Feb., Apr., May		Feb., Apr., May, June	

Annual Differences in Weight

The study of the annual differences in the length-weight relation of gizzard shad in 1952–55 was based on data for only those months during which adequate collections were made in at least two of these years. As was brought out in the previous section, the weight of shad varies with the season. Since samples were not adequate for determination of length-weight relations for every month of each year, the use of yearly data would result in a bias in favor of the year during which the specimens were obtained in the months of greatest weight. Consquently, the paired comparisons for 1952–55 were based only on data from months common to both years being compared (table 10).

Shad were heaviest in 1952 and lightest in 1953. The rating of years ran: 1952>1954>1955>1953.

LENGTHS AND WEIGHTS OF AGE GROUPS

The average size of the members of an age group varies with time of capture within the year along clearly seasonal lines. The monthly average lengths of shad show little growth in early spring, rapid growth in summer and early fall, and apparently a cessation of growth in winter for both sexes and all age groups (table 11). The course of growth becomes more apparent when portrayed graphically (fig. 8). After about June of their second year of life female shad were rather consistently longer than males of corresponding age.

The average monthly weights of shad showed, in general, a gradual decrease from the first of the year until June (table 11; fig. 9). This decline

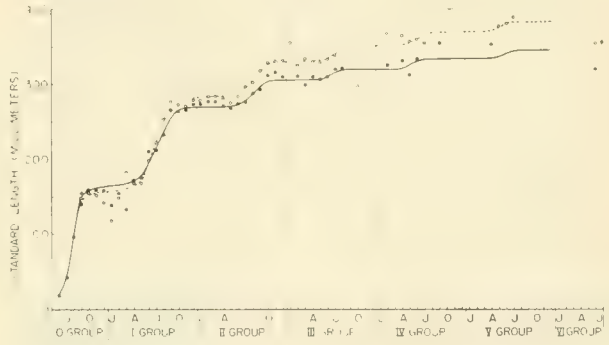

FIGURE 8.—Lengths of gizzard shad at capture in each month by age and sex. Dots are empirical averages of standard length. Open dots represent females; solid dots, males. Curves were drawn by inspection.

was followed by a rapid rise in late summer and fall. Seasonal variation of the length-weight relations (see earlier section) contributed to these changes. The female shad were heavier than males after about June of their second year of life.

The average monthly lengths of the O-group shad warrant special comment. Because some gizzard shad can be found in the spawning state in western Lake Erie from early June to mid-July (see section on length of spawning season), every sample of young shad collected usually contained fish hatched over a period of time, the extremes of which often differed in age by as much as a month or more. The successive collections continually yielded low average changes in length because of the great percentage of the newer, smaller shad constantly added to the population. This bias was aggravated by the tendency of the larger O-group fish to move off-

TABLE 11.—*Average standard lengths and weights of gizzard shad at capture*

Month of capture	O group		I group				II group				III group				IV group				V group				VI group			
			Length		Weight		Length		Weight		Length		Weight		Length		Weight		Length		Weight		Length		Weight	
	Length	Weight	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	Male	Female
	Mm.	*G.*	*Mm.*	*Mm.*	*G.*	*G.*	*Mm.*	*Mm.*	*G.*	*G.*	*Mm.*	*Mm.*	*G.*	*G.*	*Mm.*	*Mm.*	*G.*	*G.*	*Mm.*	*Mm.*	*G.*	*G.*	*Mm.*	*Mm.*	*G.*	*G.*
Jan.			133	123	53	42	282	292	503	585		*356		*1,169												
Feb.			*146	129	*69	48	274	283	479	539	314	*305	705	*714	*325	*368	*798	*1,253								
Mar.			*133	*198	*52	*174	280	282	519	515	*298	*334	*574	*865												
Apr.			165	165	85	84	269	279	406	473	308	328	631	835	*324	*364	*678	*1,072	*354		*809					
May			167	160	87	77	267	269	384	411	303	329	540	750	*312	*356	*623	*911		*378		*1,040				
June	18	0.1	195	204	158	188	272	283	396	503	310	333	592	778	333	358	691	926		*382		*1,082	*321	*355	*729	*1,114
July	38	0.7	213	218	232	249	275	294	442	572	320	338	626	854		*355		*1,008		*390		*1,350	*357		*810	
Aug.	61	28	232	241	294	356	285	302	531	687	*313		*636													
Sept.	119	79	258	268	408	446	*303	*317	*568	*722		*360		*1,162	*355		*897									
Oct.	152	84	264	265	441	457	312	330	750	871																
Nov.	152	86	261	269	424	469	*316	*330	*756	*996																
Dec.	138	66	270	273	468	500	*310	*335	*816	*966																

*Asterisk indicates an average based on fewer than five fish.

shore from the sampling area and their growing ability to avoid capture. As a consequence, the sequence of these low average monthly lengths cannot be construed to indicate the rate of growth for these young shad. It was held desirable, therefore, to estimate the position of certain points and of the curve in the preparation of figure 8. No precise quantitative justification can be given for these estimates, but they were based on broad sampling experience and extensive observations on catches in inshore waters. The estimates are held surely to be superior to judgment based on the sadly biased sample records. The curve and points of figure 8 beyond age-group O are based strictly on the records of table 11. The records of monthly growth of table 12 were read from the curve of figure 8.

Gizzard shad of age-group O presumably grew most rapidly in July, August, and September and had peak growth in August. The record for I- and II-group shad indicates that growth in length of the I-group fish progresses rapidly earlier in the year than it does for the II-group. Greatest gain occurred a month earlier—in July. Growth was slight for both groups during May and for the I-group after September.

During the second year of life the male shad grew in length 57 percent as much as during the first year, and in the third year, 28 percent as much. For the female shad the second- and third-year growths were 66 percent and 34 percent, respectively, of the first-year growth.

Seasonal changes in weight resemble those in length (compare figs. 8 and 9) except that weight decreases over winter from the peak attained during the previous fall. The basis for this change was explained earlier in the section on seasonal changes in weight.

Attempts to follow seasonal growth of gizzard shad by use of tagged individuals were unsuccessful. No fish were recaptured from some 600 tagged during the winter of 1952.

CALCULATED GROWTH

Calculated Lengths of Age Groups

The dependability of calculations of length at time of annulus formation is indicated by comparison of the calculated lengths and the lengths of shad which were captured between the end of the growing season and the time of annulus formation (first and last columns of table 13). Because the annuli are the only landmarks on the scale which can be related to a somewhat definite time, and because the shad has practically the same length from the beginning of the calendar year to the time of the annulus formation, the length of a shad captured in this period should agree closely with the length calculated from an older fish to the corresponding annulus.

Agreement was close among adequately represented age groups except for the I-group shad. In the compilation of the empirical data for this group, 105 shad had to be eliminated because sex could not be determined with certainty; their average standard length was 129 mm. Had they been included, the disagreement between empirical and calculated lengths would have been less, but

TABLE 12.—*Progress of season's growth in length of gizzard shad by millimeters and percentage*

[Lengths taken from the curves of figure 8]

Period	O-group				I-group								II-group							
					Male				Female				Male				Female			
	Average length	Increment of growth	Accumulated growth	Growth during month	Average length	Increment of growth	Accumulated growth	Growth during month	Average length	Increment of growth	Accumulated growth	Growth during month	Average length	Increment of growth	Accumulated growth	Growth during month	Average length	Increment of growth	Accumulated growth	Growth during month
	Mm.	*Mm.*	*Percent*	*Percent*	*Mm.*	*Mm.*	*Percent*	*Percent*	*Mm.*	*Mm.*	*Percent*	*Percent*	*Mm.*	*Mm.*	*Percent*	*Percent*	*Mm.*	*Mm.*	*Percent*	*Percent*
Apr. 30					167	0	0	0	164	0	0	0	263	0	0	0	273	0	0	0
May 30	[1] 5	5	3	3	175	8	8	8	175	11	10	10	266	3	6	6	276	3	5	5
June 30	22	17	13	10	199	24	33	25	204	29	37	27	271	5	17	11	282	6	16	11
July 30	50	28	30	17	225	26	60	27	233	29	64	27	282	11	40	23	294	12	38	22
Aug. 30	114	64	69	39	249	24	85	25	257	24	85	21	297	15	72	32	309	15	65	27
Sept. 30	155	41	94	25	258	9	95	10	268	11	95	10	305	8	89	17	320	11	85	20
Dec. 30	165	10	100	6	263	5	100	5	273	5	100	5	310	5	100	11	328	8	100	15

[1] These fish are assumed to be about a week old. Shad hatched in the laboratory were 3.5 mm. in standard length and became 5.2 mm. long in 4 days.

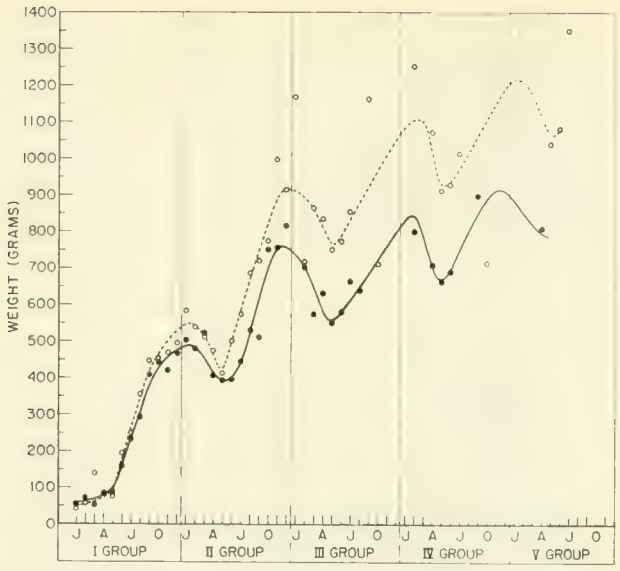

FIGURE 9.—Weights of gizzard shad at capture in each month by age and sex. Dots are empirical averages. Open dots represent females; solid dots, males. Curves were drawn by inspection.

still substantial. The principal cause of the discrepancy was probably the selective sampling of age-group I. Many of this group were too small to be caught by the gill nets and the trap nets. At the higher ages the agreement between empirical and calculated lengths was good. The lengths calculated for each year of life from progressively older shad show a similar close agreement except for the first year of life.

No year classes exhibited consistently fast or slow growth in length, nor did growth appear to have been outstandingly good or bad in any particular calendar year.

Compensatory Growth in Length

It has been observed frequently that although the larger of the young fish maintain a length advantage over the smaller ones during subsequent growth, the smaller young fish grow more rapidly during subsequent years than the larger ones and, thus, reduce progressively the original length difference.

To study this "compensatory growth" in gizzard shad, I tabulated the annual increments of growth of III-group fish, arranged by 20-mm. groupings of length at the end of the first year of life (table 14). The sexes were treated separately, and only fish caught in 1954 were used. In both sexes the annual increments generally varied inversely with first-year length; consequently, the difference in length between the shortest and the longest first-year fish diminished progressively to a minimum in the third year.

TABLE 13.—*Comparison of the average empirical standard length of gizzard shad with average length calculated for each year of life for each age group for each sex*

[Fish of the same age were combined without regard for year classes. Empirical lengths are given only for shad captured between the end of the growing season and the time of annulus formation. Number of fish in parentheses]

Sex and year of life	Average empirical length	Age group					Average calculated lengths [1]
		I	II	III	IV	V	
Male:	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm*	*Mm.*
First	165	146	130	145	146	139	141
	(227)	(76)	(92)	(34)	(8)	(2)	
Second	273	------	270	282	270	270	273
	(530)	.. ..	(37)	(34)	(8)	(2)	
Third	313	....	------	316	312	310	313
	(53)	-----	------	(5)	(8)	(2)	
Fourth	328	.	-----	------	348	337	343
	(8)	...	-----	----	(1)	(2)	
Fifth	350	...	..	. ...	-----	349	349
	(1)	.. ...	. ....	------	------	(1)	
Females.							
First	162	134	139	146	144	138	140
	(267)	(71)	(118)	(62)	(13)	(3)	
Second	283	. .	285	292	280	282	285
	(489)	...	(57)	(62)	(13)	(3)	
Third	335		-----	336	333	336	335
	(83)	.	------	(42)	(13)	(3)	
Fourth	361		. .	-----	362	369	366
	(17)	. . .	. ....	------	(6)	(3)	
Fifth	383	.	..	-----	....	390	390
	(4)	....	..	..	....	(1)	

[1] Unweighted means.

TABLE 14.—*Average annual increments of length of III-group shad of the 1954 collections arranged by 20-mm. groups of first-year calculated length*

[Second- and third-year calculated lengths given in parentheses]

Males				Females			
Number of fish	First year	Second year	Third year	Number of fish	First year	Second year	Third year
	Mm.	*Mm.*	*Mm.*		*Mm.*	*Mm.*	*Mm.*
1	96	161	49	.. ..	....	--	
	. . .	(257)	(306)	.. ..	....	....	..
4	109	162	36	9	114	169	50
	------	(271)	(307)	... .	....	(283)	(333)
10	132	151	31	12	131	160	45
	...	(283)	(314)	..	....	(291)	(336)
10	154	131	28	22	152	139	43
	....	(285)	(313)	... .	.	(291)	(334)
3	173	114	31	13	166	135	38
	..	(287)	(318)	... .		(301)	(339)
4	185	105	25	3	184	124	36
	....	(290)	(315)	. .		(308)	(344)
Difference in standard length [1]	89	33	9		70	25	11
Difference in length increments [1]	..	56	24		.	45	14

[1] Between shortest and longest first-year groups

REPRODUCTION AND EARLY DEVELOPMENT

Size and Age at Maturity

The sex and maturity of gizzard shad were always determined by dissection except for those fish from which eggs or milt were flowing during the spawning season. Vladykov (1945) stated that the males have darker fins than the females, but I found that neither this nor any other readily discernible external characteristic indicated the sex with reasonable consistency for all age groups in all seasons. Generally, however, one might expect a shad that is relatively deep for its length to be a female. Since the time of this study, Moen (1959) sexed gizzard shad by examining the urogenital opening with a probe.

The sex of large fish was determined easily—the testes were opaque white, whereas, the ovaries were mostly semitranslucent and light yellow or pink. Sex determination was more difficult in small shad. Here, the testes were whitish and the ovaries almost colorless and translucent, but the distinction between them became less and less apparent as one examined smaller and smaller gonads. After much study (comparisons of judgments from macroscopic examination with subsequent determinations from histological sections) I could frequently distinguish the sexes macroscopically when the diameter of the gonad was only 1 mm. and readily when it attained 2 mm. The minimum standard length of fish for which sex could be determined macroscopically with confidence was about 120 mm. (4 or 5 months old), although on occasion sex could not be determined for a larger shad.

Although a fish whose milt or spawn flows during the spawning season is sexually mature, the absence of this feature does not indicate immaturity. In this situation, during the spawning season or any other time, different criteria must be employed. Histological studies of ovaries collected throughout the year have enabled me to recognize a potential spawner several months in advance of the spawning season and spent females as long as a month after spawning. Moreover, the relation of the histological characteristics of the ovary to the gross appearance of that organ made possible an estimate of maturity by gross observations. In females that will not spawn, the ovaries contain only minute, scarcely visible eggs, whereas potential spawners exhibit, in addition to the minute eggs, fair-sized ones that are clearly visible within the semitranslucent ovary several months prior to spawning. Although completely spent females have only the minute eggs that are characteristic of the ovaries of fish which will not spawn, their ovaries for a few weeks after spawning are more flaccid than those of nonspawners, the minute eggs are some little distance apart, and the interovular spaces have a more watery appearance.

The maturity of males could not be determined in the absence of flowing milt. The presence of motile sperm, obtained by lancing a testis, does not assure maturity. Males examined in January had motile sperm—even the I-group males, most of which would not spawn in the spring. Maturity in males is undoubtedly associated with structural development or physiological change which permits release of the sperm. The great scarcity of I-group males at the spawning site in May and June suggests that this release mechanism does not usually become functional in males of that age. The presence of a few of them on the spawning grounds during July may indicate that some have matured near the end of the spawning season.

In 1954, I found three mature I-group female shad. Their standard lengths were 197, 225, and 236 mm. Some 25 or 30 I-group males, 190 to 230 mm. long, also were mature. The milt and spawn produced by fish of this age were scanty. The crosssection of an ovary of a mature I-group female reveals few mature eggs (fig. 10).

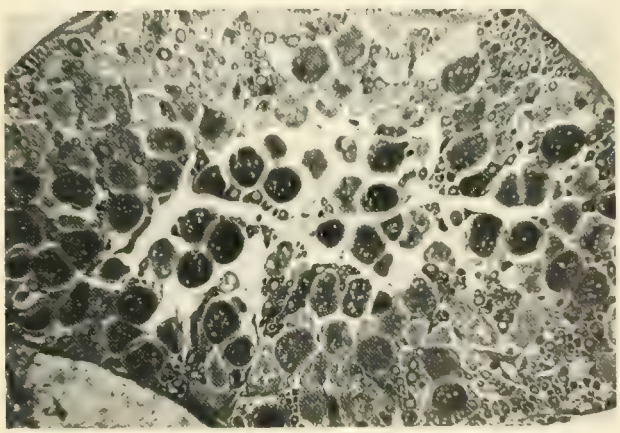

FIGURE 10.—Cross section of an ovary of a mature I-group gizzard shad showing relatively few near-mature eggs (July 6, 1954).

Invariably, these precocious fish arrived at the spawning site in July, near the end of the spawning season. They were not the largest of their age group, whose length range extended to 254 mm. at this time, but were generally above the average length. They obviously represented only a fraction of their group, but the exact percentage could not be determined because segregation according to maturity is great during the spawning season.

Most spawners were in their third year of life (II group), but not all shad of this age group spawned. The average length of the June 1954 II-group females that would have spawned (29 cm.) was 1 cm. greater than that of the shad which would not have spawned during the current year (28 cm.). Although the percentage of the female shad that matured during their third year of life could not be determined because of the segregation according to maturity, observations on gonads of shad captured throughout the year indicated that at least 80 percent of them became mature at this age in western Lake Erie. Only rarely were female shad older than the II-group immature. With few exceptions, the II-group male shad had well-developed testes. Since, however, I was unable to determine maturity in the absence of flowing milt, I could not distinguish a spent individual from one which had not spawned—in fact, could not judge from the state of the testes in any month the percentage of mature males of any age group.

TABLE 15.—*Sex ratios for gizzard shad for which both sex and age were determined monthly*

[These shad were captured in the vicinity of the Bass Islands in 1952–55]

Month and sex	Age group							Total for month
	0	I	II	III	IV	V	VI	
January:								
Male		7	14					21
Female		7	31	1				39
Percentage males		50.0	31.1	0.0				35.0
February:								
Male		8	135	5	2			150
Female		15	104	3	1			123
Percentage males		31.8	56.5	62.5	66.7			54.9
March:								
Male		1	5	3				9
Female		2	10	2				14
Percentage males		33.3	33.3	60.0				39.1
April:								
Male		151	156	17	3	1		328
Female		177	164	16	4			361
Percentage males		46.0	48.8	51.6	42.9	100.0		47.6
May:								
Male		48	90	8	4			150
Female		69	128	7	3	1		208
Percentage males		41.0	41.3	53.3	57.1	0.0		41.9
June:								
Male		21	913	65	4		1	1,004
Female		21	753	62	10	2	1	849
Percentage males		50.0	54.8	51.2	28.6	0.0	50.0	54.2
July:								
Male		121	172	5			1	299
Female		166	315	24	4	1		510
Percentage males		42.2	35.3	17.2	0.0	0.0	100.0	37.0
August:								
Male	119	104	13	1				237
Female	116	100	13					229
Percentage males	50.6	51.0	50.0	100.0				50.9
September:								
Male	410	118	4	1	1			534
Female	516	159	3					678
Percentage males	44.3	42.6	57.1	100.0	100.0			44.1
October:								
Male	319	123	9					451
Female	352	99	6	1				458
Percentage males	47.5	55.4	60.0	0.0				49.6
November:								
Male	827	73	1					901
Female	876	92	1					969
Percentage males	48.6	44.2	50.0					48.2
December:								
Male	221	37	1					259
Female	276	60	4					340
Percentage males	44.5	38.1	20.0					43.2
Total in age groups:								
Male	1,896	812	1,513	105	14	1	2	4,343
Female	2,136	967	1,532	116	22	4	1	4,778
Percentage males	47.0	45.6	49.7	47.5	38.9	20.0	66.7	47.6

Sex Ratio

The gizzard shad captured in the vicinity of the Bass Islands in 1952–55 for which sex could be determined were combined to show trends of the sex ratio by month and by age (table 15).

Only limited seasonal trends are apparent from the data on sex ratio; the month-to-month fluctuations were decidedly irregular.

Among the 10 months in which the total samples exceeded 250 fish, July stands apart because of the small percentage of males (37.0 percent). Among the other 9 months, this percentage ranged between 41.9 (May) and 54.9 (February). The percentage for all 12 months was 47.6.

The percentage of males varied little among the four younger age groups (45.6–49.7 percent males) in the combined sample for all months, but males became less numerous at the higher ages (38.6 percent in age groups IV–VI, combined).

Information on the percentage of males in samples from the shallow waters of Fishery Bay and the deeper waters of the lake gives no indication of segregation of the sexes within the lake except for age groups II and III (shad of spawning age) during June. The records for that month (table 16) suggest that males are relatively more plentiful at the spawning site than in the deeper water. The data on sex ratio on the spawning site during the spawning season are undoubtedly biased in favor of the males since their greater activity increases the likelihood of capture by the stationary fishing gear. This bias, however, does not account entirely for the large percentage of males

TABLE 16.—*Sex ratios for gizzard shad caught in the shallow waters of Fishery Bay and in the deeper waters of Lake Erie for June and for all other months combined in 1952–55*

Month and site of capture	Sex	Age group							Total
		0	I	II	III	IV	V	VI	
June:									
Bay	Male		5	610	47	3			665
Do	Female		6	207	16				229
Do	Percentage males		45.6	74.7	74.6	100.0			74.4
Lake	Male		16	303	18	4		1	342
Do	Female		15	546	46	10	2	1	620
Do	Percentage males		51.6	35.7	28.1	28.6	0.0	50.0	35.6
All months except June:									
Bay	Male	63	214	154	6	1			438
Do	Female	82	207	196	6	2			493
Do	Percentage males	43.4	50.8	44.0	50.0	33.3			47.0
Lake	Male	1,833	577	446	34	6	1	1	2,898
Do	Female	2,054	739	583	48	10	2		3,436
Do	Percentage males	47.2	43.8	43.3	41.5	37.5	33.3	100.0	45.8

on the spawning site; in the deeper waters the percentage of males is greater between spawnings than during the spawning season.

The sex ratios of mature shad captured in Fishery Bay and in the deeper waters of the lake within 7- or 8-day periods in May, June and July of 1954 and 1955 (table 17) indicate that the percentage of males in the population of shad captured in the bay increased during early and mid-June and reached a high in the third quarter; the females were relatively most numerous in the last quarter. Males were scarce in deeper water in June (exception, June 9–15), and with the exception of one sample (July 16–23), this scarcity continued through July. Data are few on the sex ratio in Fishery Bay in July; females predominated strongly in the single sample. The generally small percentages of males in all July samples account for the low monthly percentage for July, mentioned in the earlier description of table 15.

TABLE 17.—*Sex ratios for mature gizzard shad captured in the shallow waters of Fishery Bay and the deeper waters of Lake Erie during May, June, and July, 1954 and 1955*

Time of capture	Bay			Lake		
	Male	Female	Males	Male	Female	Males
May:	*Number*	*Number*	*Percent*	*Number*	*Number*	*Percent*
1–8	1	1	50.0	23	32	41.8
9–15	5	7	41.7	29	44	39.7
16–23	1	2	33.3	28	39	41.8
24–31	5	0	100.0			
1–31	12	10	45.5	80	115	41.0
June:						
1–8	135	52	72.2			
9–15	142	48	74.7	49	34	59.0
16–23	261	42	86.1	96	247	28.0
24–30	122	82	59.8	181	346	34.1
1–30	660	224	74.7	326	627	34.2
July:						
1–8	58	95	37.9	84	170	33.1
9–15				8	15	34.8
16–23				23	14	62.2
24–31				2	5	28.6
1–31	58	85	37.9	117	204	36.4

DEVELOPMENT AND MATURATION OF THE EGG

For convenience in description, the development of the egg has been divided arbitrarily into six stages (fig. 11). The following descriptions were made from ovary sections fixed in Bouin's solution and stained with hematoxylin and eosin.

Stage 1.—The young oöcyte is 10 to 20 μ in diameter and has a large nucleus with a centrally located nucleolus. The nucleolus and nuclear membrane stain darkly with the hematoxylin, while the cytoplasm and the nucleoplasm stain with eosin.

Stage 2.—The oöcyte, now 20 to 70 μ in diameter, has not yet acquired its follicle-cell envelopment. The nucleus has grown at a faster rate than the cytoplasm. This cytoplasm is now accepting some of the hematoxylin, while the ground substance of the nucleus still stains with eosin. The nucleolus, if present, is lost among the darkly staining chromatin materials which are somewhat scattered throughout the nucleus.

Stage 3.—This stage includes oöcytes which range from 0.07 mm. to 0.15 mm. in diameter. The nucleus and cytoplasm appear to have grown at the same rate from the last stage. The cytoplasm now stains darkly with hematoxylin; the nuclear sap stains pink. The dark-staining chromatin material is more plentiful and is arranged circumferentially along the periphery of the nucleus. Flat follicle cells are arranged as a single-celled layer around the oöcyte.

Stage 4.—The follicle is mostly in the 0.15-to 0.30-mm. size range in this stage. The dark-staining cytoplasm is growing more rapidly than the nucleus. As the follicle approaches the 0.30-

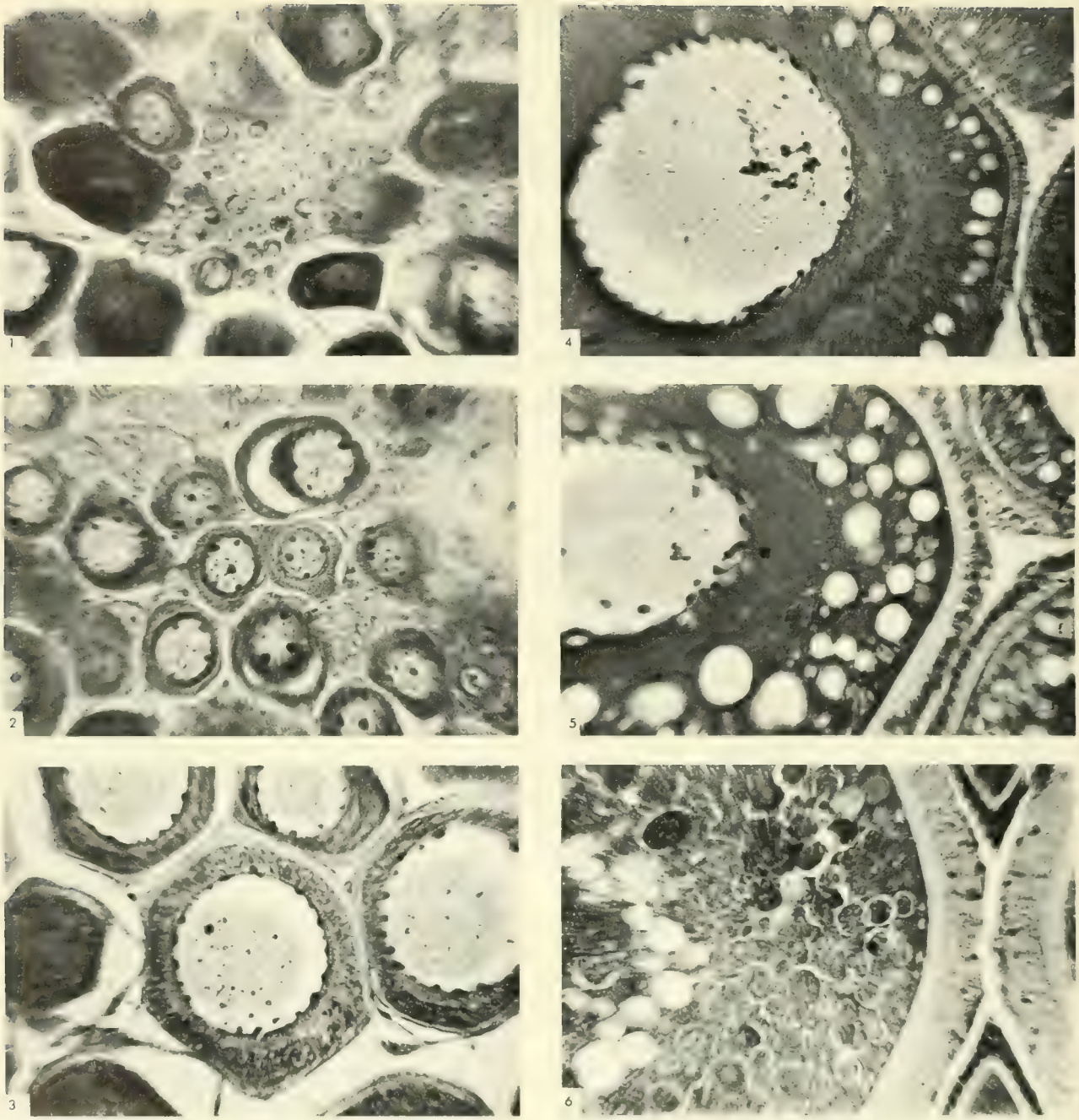

FIGURE 11.—Growth and maturation of gizzard shad eggs.

mm. size, the oöcyte's cytoplasm is stained by both hematoxylin and eosin—the resulting reddish-purple oöcyte is clearly noticeable among the bluish-purple smaller oöcytes. The nuclear membrane and chromatin material surrounding the pink-staining nucleoplasm appear fuzzy as though disintegrating. Oil globules have formed in the periphery of the cytoplasm beneath the follicle cells that have become cuboidal.

Stage 5.—In this stage the oöcyte with its envelope of follicle cells -now columnar—grows from 0.30 mm. to about 0.45 mm. The nuclear membrane has largely disintegrated, and chromatin material has all but lost its discreteness.

The peripherally formed oil globules have become larger and are moving toward the nuclear area. Small yolk granules have appeared, some of which have encroached upon the nuclear area, making this area smaller than it was in the preceding stage. These yolk granules stain mostly with eosin, while the cytoplasmic ground substance stains with both dyes. A homogeneous vitelline membrane has made its appearance between the oöcyte and its surrounding follicle layer.

Stage 6.—During this stage the follicle size is between 0.45 mm. and 0.50 mm. The nuclear membrane and chromatin material are no longer evident; the oil globules have migrated around the nuclear area and encroached upon it so that the area now is relatively small. During this migration, the yolk granules have moved away from the central area, leaving this area surrounded by oil globules. The small yolk granules of the previous stage have now become very coarse. The vitelline membrane under the single-celled follicle layer is now thick and prominent.

Up to this stage the oöcyte appeared to be isolecithal since the nucleus occupied a central position as long as it was evident and the amount of yolk compared with the size of the nucleus did not seem to be plentiful. Just prior to spawning, however, the oil globules almost completely disappear and the cell is so packed with large yolk granules that no definite nuclear region is recognizable. The tremendous amount of yolk, despite the lack of information regarding the location of the nucleus, suggests that the oöcyte now is telolecithal.

Before the egg leaves the ovary, the single-celled follicular layer ruptures and separates from the vitelline membrane. The former remains in the ovary where it gradually disintegrates. The vitelline membrane becomes greatly distended by imbibed water after the egg is spawned and water-hardened.

Most of the O-group gizzard shad already had oöcytes in Stages 1 and 2 as early as October. After they appeared, they were a constant feature in the ovary; they were most abundant in the fall in O-group fish, somewhat less abundant in older fish immediately after spawning, and least plentiful in ripe fish. In the O-group shad the oöcytes begin development so late in the season that usually they do not progress beyond Stage 2 by late fall; there is an accumulation of Stages 1 and 2. Older shad which spawned, however, showed no such accumulation, for the oöcytes that formed earliest had time to progress to later stages. Their constant presence—though they are not plentiful in near-ripe and ripe fish—indicates that one or both of the following processes must occur: these early stages are continually being formed, perhaps at varying rates; or the oöcytes formed later in the generative season—if there be one—remained more or less dormant throughout the remainder of the season—the nutrients being diverted to the earlier formed, more advanced oöcytes.

In shad which had spawned, oöcytes in Stages 3 and 4 are found in late fall and winter, but in the youngest shad (I group after January) they appear in spring.

Stages 5 and 6 usually do not appear in the I-group fish; they are present in spring in the II-group shad, and are found in spring and early summer in the older females.

SEASONAL CHANGES IN THE OVARY

The seasonal changes in the ovary of every gizzard shad are much the same after the first spawning, which occurs usually in II-group fish. Changes preliminary to first spawning follow a different course.

During fall, the oöcytes of O-group fish appear late and progress so slowly that by the time the spawning season arrives (fish are now I-group) the eggs are not mature enough to be spawned. In a few fish of this age (presumably those which hatched very early) some of the eggs become mature and are spawned late in the spawning season (fig. 10). In a few others, the eggs become mature too late to be spawned and are resorbed (fig. 12). In most of these I-group fish, however, most of the eggs have developed to Stage 4 (fig. 11), and remain at that stage until the next spawning season approaches.

For convenience, the ovarian changes of gizzard shad after their first spawning have been divided into six stages (fig. 13).

Stage A.—In late July, August, and early September, the shrunken ovary is filled with oöcytes in Stages 1, 2, and 3. The germinal epithelium extends inward from the periphery of the ovary in irregular layers. The central cavity of the saccular ovary is highly variable and

is much branched. The branches extend between the layers of the germinal epithelium.

Stage B.—From late September to early November the ovary contains a greater proportion of oöcytes in Stage 3 than earlier in the season. Some oöcytes of Stage 4 are also present.

Stage C.—During winter and early spring the ovary contains some oöcytes in Stage 5, a great many in Stage 4, and decreasing numbers in the earlier stages.

Stage D.—In April, May, and early June the ovary has oöcytes mostly in Stages 5 and 6; those in Stage 6 become more and more predominant toward the close of this period. Some oöcytes in Stages 1 and 2 also are present. Those in Stages 3 and 4 are rare. The central cavity of the ovary is obliterated by the dense packing of the large oöcytes.

Stage E.—In June, the eggs in the ovary are in a stage subsequent to the last stage shown in figure 11—some are ready to be spawned. That others have left the ovary is apparent from the empty spaces and the follicular remnants. Oöcytes in Stages 1 and 2 are present—a few in Stages 5 and 6 may still be found.

Stage F.—Immediately after spawning and perhaps for a week or two later the ovary contains remnants of the old follicular layers. The oöcytes present are mostly in Stages 1 and 2, but some have already reached Stage 3.

The seasonal progression of ovarian change by no means proceeds at the same rate in all gizzard shad. The figures represent the situation for most shad in western Lake Erie. In some of the fish the stages are months in advance of those given in the figure; in others, they are months tardy. Nevertheless, differences among individuals decrease as the spawning season approaches. Fish with advanced rates exhibit slower development just prior to the spawning season, but development proceeds rapidly in fish with retarded rates.

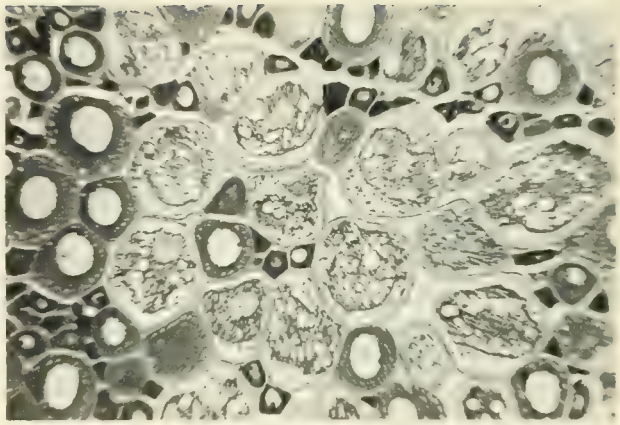

FIGURE 12.—Unspawned eggs being absorbed while new eggs are developing (I-group gizzard shad, December 16, 1953).

Fecundity

The number of eggs per individual varied considerably (table 18). Although the number of counts is meager, the averages for the age groups definitely show low egg production among the precocious I-group shad, a maximum production by the II-group fish, and slowly declining numbers among successively older age groups.

TABLE 18.—*Number of eggs per individual gizzard shad of different sizes and ages*

Age and date of capture	Standard length	Weight	Ovary weight	Estimated eggs per fish	Eggs per gram of fish	Eggs per gram of ovary	Ovary as percentage of fish weight
	Mm.	*G.*	*G.*	*Number*	*Number*	*Number*	*Percent*
Age group I:							
July 6, 1954	225	260	3.9	22,400	86	5,744	1.5
July 8, 1954	236	305	14.8	96,560	317	6,524	4.8
Average	231	283	9.4	59,480	210	6,328	3.3
Age group II:							
May 23, 1955	282	524	78.6	543,910	1,038	6,920	15.0
June 3, 1954	285	529	71.7	524,580	992	7,316	13.6
May 20, 1954	292	593	35.2	211,380	356	6,005	5.9
May 20, 1954	293	578	24.6	258,350	447	10,502	4.3
May 23, 1955	305	526	55.8	356,710	678	6,393	10.6
Average	291	550	53.2	378,990	689	7,124	9.7
Age group III:							
May 23, 1955	322	713	44.5	406,170	570	9,128	6.2
June 18, 1954	328	700	62.6	367,670	525	5,873	8.9
June 24, 1954	343	847	36.2	260,510	308	7,196	4.3
Average	331	753	47.8	344,780	458	7,213	6.4
Age group IV:							
June 18, 1954	348	882	28.8	267,220	303	9,278	3.3
June 23, 1954	363	895	74.2	350,280	391	4,721	8.3
Average	356	889	51.5	308,750	347	5,995	5.7
Age group VI:							
June 23, 1954	355	1,114	29.8	215,330	193	7,226	2.7

As the fish become older, their ovaries acquire increasing amounts of connective tissue; hence, they should produce fewer eggs per gram of ovary with increase in age. This anticipated change is not borne out, however, in table 18. The per-gram-ovary yield of eggs was highly variable, even among the fish of an age group. The situation is not surprising since the problem of finding differences is compounded by the fact that the ovaries were in varying stages of development at the time the fish were captured. An ovary contains a certain number of eggs which would be spawned during the coming spawning season. These eggs, together with immature ones and other components of the ovary, make up the weight of the ovary. The farther along these eggs develop the heavier they become; the weight of the ovary increases and its per-gram yield of eggs decreases.

On the per-gram-of-fish basis the older fish do, indeed, produce fewer eggs than the younger ones (except the precocious I group). The "relative fecundity" tripled from the I group to the II group and then declined to age-group VI which had about the same value as the I group.

On the basis of fish size it would appear that fish weighing 500–600 g. produce more eggs than do those whose weights fall either below or above that range. The productivity of these fish may be the result of age rather than size, however; in the table only the II-group shad occupy this range. Further information on this possibility was gained from 69 II-group female shad, captured in the first two quarters of June 1954; their weights ranged from 339 to 733 g. They were divided by 50-g. groupings (301 to 350, 351 to 400, —), and the ratio of ovary weight to fish weight was calculated for each group. (Egg counts had not been made on these fish.) The ratio was highest for the 500- to 600-g. fish. This finding would suggest, then, that fish in this weight range produce the most eggs.

Spawning

The single spawning site of gizzard shad that I was able to find was a bar some 200 feet long and covered by 2 to 4 feet of water near Put-in-Bay. The bottom is topped with sand, gravel, and boulders. *Cladophora*, *Myriophyllum*, and *Butomus umbellatus* (forma *vallisneriifolius*) are abundant during the spawning season.

No gizzard shad were found on this bar in 1954 prior to, or after, the spawning season. To learn the day-to-day variations of the numbers of shad there during the 1955 spawning season, I set a 100-foot, 4-inch-mesh gill net nightly along the top of the bar from May 9 to June 30. The catches, together with the water temperatures, are recorded in table 19.

It was evident later that the female shad does not spawn her entire egg holdings in one visit to the bar. Consequently, some shad would probably have visited the bar more than once during the season had they not been caught. Furthermore, gizzard shad exhibit greater activity at the height of spawning than just prior to it or afterwards. Hence, greater percentages of those present in a given area are likely to swim afoul of the net at this time than at other periods. The table must be interpreted with these points in mind.

Temperature clearly is important in the onset and progress of spawning. Gizzard shad first appeared in the net on this bar at a temperature of 59° F. and were common at about 67° F. Indeed, when the water temperature dropped slightly (to 65° and 65.5° F. on June 12–15) the numbers of shad also dropped.

To define the spawning site more precisely, I set gill nets transversely across the bar. In every

TABLE 19.—*Water temperatures and daily captures of shad by a 100-foot, 4-inch-mesh gill net set on a spawning site in Fishery Bay in May and June 1955*

[The net was lifted daily at 9 a.m. except on June 2–11 (see text); the water temperature was read at the time of lifting]

Date	Shad caught	Water temperature	Date	Shad caught	Water temperature
	Number	° *F.*		*Number*	° *F.*
May 10		58.0	June 5	12	66.0
11		59.0	6	21	67.5
12		58.5	7	23	66.5
13		60.0	8	24	65.5
14		60.0	9	5	66.5
15		59.0	10	10	66.5
16		61.5	11	16	66.0
17		59.5	12	6	65.5
18		59.0	13	4	65.0
19	1	59.0	14	1	65.5
20		60.0	15	1	65.5
21		61.0	16	14	68.0
22		61.0	17	57	70.0
23		61.0	18	35	71.0
24		61.0	19	38	71.5
25		61.5	20	20	72.0
26		61.0	21	10	71.0
27		62.5	22	10	71.5
28		63.0	23	4	72.0
29	1	63.0	24	33	72.5
30		62.0	25	24	73.0
31		63.0	26	5	73.0
June 1	4	64.0	27	10	74.0
2	6	65.5	28	5	73.5
3	20	67.0	29	18	73.5
4	10	66.0	30	17	73.0

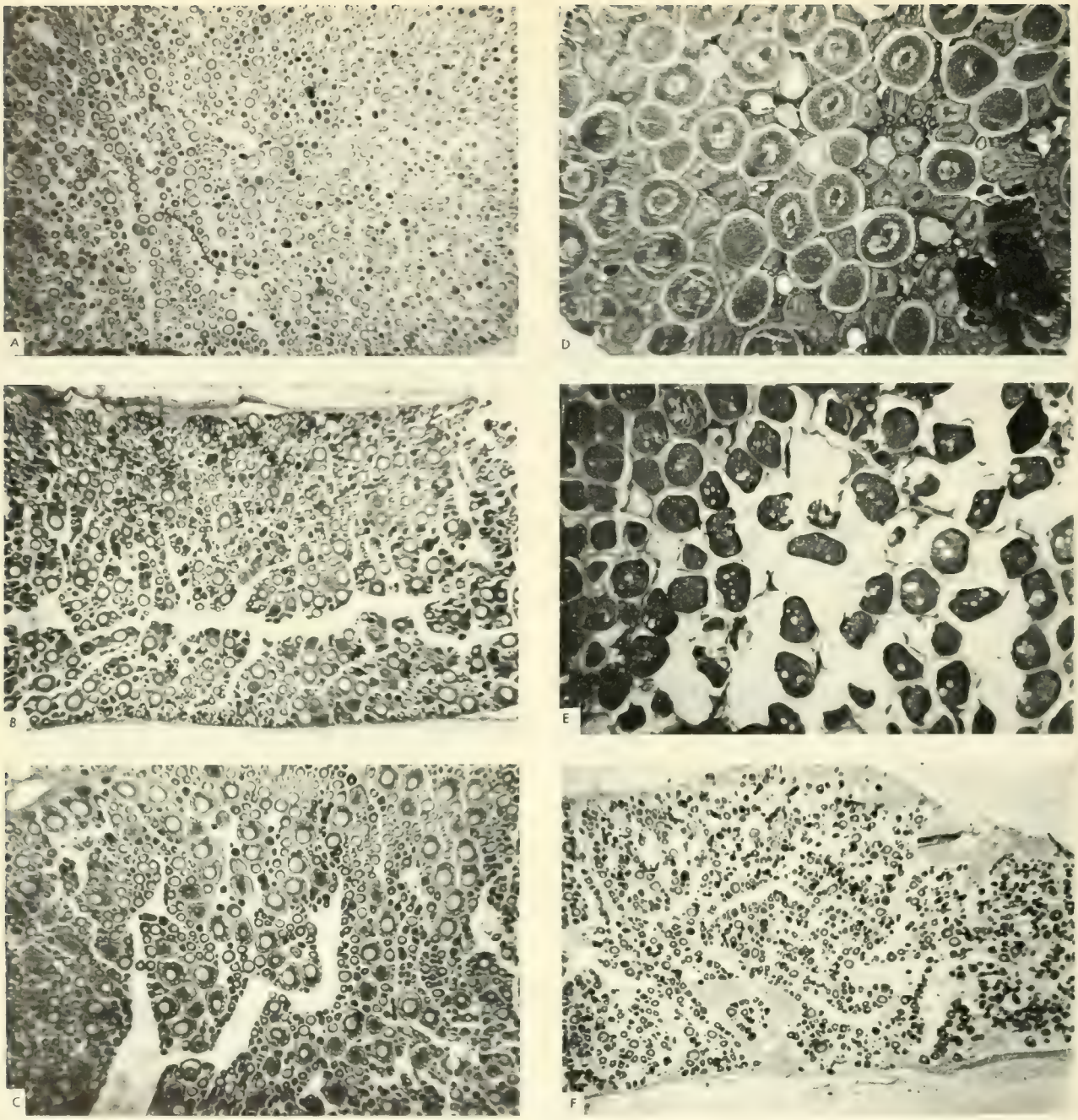

FIGURE 13.—Six stages in the seasonal changes in the ovary of gizzard shad.

lift most of the gizzard shad were caught in that portion of the net that crossed the highest area of the bar, and fewer at the ends of the nets where they sloped gradually into deeper water.

The conditions described here must not be taken as the only ones under which gizzard shad may spawn. Although I have little information on possible shad spawning in the lake, and have never taken shad eggs in plankton nets in the open lake, gill nets and trap nets sometimes have had eggs of gizzard shad and other fish adhering to them during the spawning season. The females may have forced spawn from themselves during their attempts to escape from the gill nets or they

may have been held beyond their spawning time in the trap nets, which were lifted only every other day.

It is also probable that some gizzard shad are not able to find a suitable spawning site by the time the eggs are ready to be expelled. This possibility is supported by the observation that some of the female shad caught in the lake by commercial fishermen were releasing eggs. To explore this possibility further, I determined the percentage of spawning fish for the II–group and older female shad caught in Fishery Bay and for those captured in the lake during May, June, and July 1954–55 (table 20). The state of the ovaries was determined by gross examinations. The much smaller percentages of spawning shad captured in the lake than in the bay suggest that most of the ripe females migrated from deeper to shallower water during the spawning season. This finding is not in disagreement with the earlier observation (tables 16 and 17) that the percentage of females in June was less in the shoal water than in the deeper water. The high percentage of males on the spawning reef can be explained on one or more of the logical assumptions that: greater numbers of males than females entered the shoal area from the lake; that activity was greater among the males than among the females in the shoal waters; that males individually stayed longer on the site.

When fish begin to spawn, the rise in the "spawning" category should coincide with the drop in the "nonspawning" category if the fish do not migrate from the area. Lack of this relation in the lake provides further evidence that most of the fish do not remain in the deeper water when they are ready to spawn.

The rapid rise of the "spent" category in the lake from mid-June through July, which is completely out of proportion with the drop in the "spawning" group there, indicates a return of the spent fish from shallow water to the open lake.

The data of table 20 on the percentages of nonspawning, spawning, and spent females captured in Fishery Bay and in the lake during May, June, and July 1954–55 also give a basis for the estimation of the beginning, peak, and end of the spawning season of II-group and older shad.

The earliest samples containing spawning fish were captured in the first quarter of June on the spawning bar in Fishery Bay. The percentage of spawners caught here rose from 33.3 percent in that quarter to a high of 58.3 percent in the next quarter, then dropped to 45.0 percent in the third quarter and abruptly to 1.2 percent in the last quarter of June. Spawning shad were captured from the first quarter of June to the first quarter of July inclusive.

Although I lacked samples from the lake in the first quarter of June (the commercial fishermen of South Bass Island—the source of the lake-caught gizzard shad—did not fish during the last quarter of May and the first quarter of June) the Fishery Bay sample for that quarter and subsequent samples from the lake lead me to assume that spawning fish, though never numerous, were present here at that time also.

Spent fish were first observed in the first quarter

TABLE 20.—*State of ovaries of mature II-group and older gizzard shad captured in Fishery Bay and in Lake Erie in May, June, and July 1954–55*

[Given as percentages of fish in the categories "not spawning," "spawning," and "spent"]

Time of capture	Bay				Lake			
	Females	Not spawning	Spawning	Spent	Females	Not spawning	Spawning	Spent
May:[1]	*Number*	*Percent*	*Percent*	*Percent*	*Number*	*Percent*	*Percent*	*Percent*
1–8	1	100.0	0.0	0.0	32	100.0	0.0	0.0
9–15	7	100.0	.0	.0	44	100.0	.0	.0
16–23	2	100.0	.0	.0	39	100.0	.0	.0
June:								
1–8	51	64.7	33.3	2.0				
9–15	48	37.5	58.3	4.2	34	85.3	8.8	5.9
16–23	40	30.0	45.0	25.0	208	78.8	2.4	18.8
24–30	82	30.5	1.2	68.3	322	44.4	3.1	52.5
July:								
1–8	95	33.6	7.4	59.0	170	38.8	4.7	56.5
9–15	1	100.0	.0	.0	15	33.3	.0	66.7
16–23	2	100.0	.0	.0	14	.0	.0	100.0
24–31					5	.0	.0	100.0

[1] No females captured May 24–31.

of June in the Fishery Bay samples. Thereafter, all samples from both bay and lake showed increasing percentages of spent shad during June. In July, this trend persisted among the lake samples, but in the bay samples both spawning and spent fish were absent after the first quarter and only three nonspawning ones were captured. The available data indicate that the gizzard shad in western Lake Erie spawn during June and early July; the greatest percentage of them spawn in the second quarter of June.

Records of the average ovary weight as a percentage of the fish weight, for II-group and older female shad in 1954–55 (table 21), indicate that the ovary makes little increase in weight from the time the fish are spent until the following April. During that month, feeding increases (this is the first time in winter or spring during which recognizable food has been found in the shad's gut—table 24), but the fish weight decreases (table 9). Consequently, the combination of a little ovarian growth and loss of fish weight results in a rise in the ovary-weight/fish-weight ratio. This ratio is highest either in the last quarter of May, for which I have no samples, or the first quarter of June. In this period, more fish are just ready to spawn and fewer are spawning or are spent than at any subsequent period. Then, as more fish become partly or completely spent, the average ratio drops lower. The drop in June is steady, and in the last quarter of that month the ovary weight as a percentage of body weight is again at about the April level. I have no ovary weights for July, August, and September. However, since some shad are still spawning in July and follicular remains were yet to be absorbed, I suspect the low percentage of winter samples is not reached earlier than the last of July.

TABLE 21.—*The percentage of fish in the categories "not spawning", "spawning", and "spent", and the ovary weight as a percentage of the fish weight for II-group and older female gizzard shad, Lake Erie, 1954–55*

Period	Fish	Not spawning	Spawning	Spent	Ovary/fish weight
	Number	*Percent*	*Percent*	*Percent*	*Percent*
Oct.	25	100.0	0.0	0.0	1.1
Nov.	33	100.0	.0	.0	.9
Dec.	20	100.0	.0	.0	1.5
Jan.	1	100.0	.0	.0	1.1
Feb.	4	100.0	.0	.0	1.8
March	1	100.0	.0	.0	1.5
Apr.	102	100.0	.0	.0	2.4
May 1–8	33	100.0	.0	.0	3.8
May 9–15	49	100.0	.0	.0	4.2
May 16–23	41	100.0	.0	.0	4.3
June 1–8	51	64.7	33.3	2.0	9.9
June 9–15	81	58.0	37.0	5.0	8.5
June 16–23	113	47.8	16.8	35.4	5.3
June 24–30	102	16.7	.9	82.4	2.5

[1] No samples May 24–31

The mature I-group gizzard shad spawn later than older fish. Ova of three fish captured during the 1954 spawning season (June 28, July 6, and July 8) were nearly ripe (fig. 10). These fish probably would have spawned in late July or early August, or else the ova would have been resorbed.

The eggs of the II-group fish which have been in the making for 1½ to 2 years—much longer than those of older fish—might be expected to be spawned earlier than those of older fish. Information on the older shad is too scanty, however, to permit study of this possibility.

The weight of the fish appeared to have no effect on the time of its spawning.

I tried two methods to determine the time of spawning within a 24-hour period. In one, a gill net was set on the previously mentioned spawning bar in the afternoon, lifted at midnight, reset immediately, lifted in the morning, reset again, and lifted in the afternoon. The numbers of shad of each sex were tabulated for each period. In the other method, concrete slabs with a surface area of 1 square foot were lowered to the bottom at the spawning site and examined for shad eggs three times daily, when the gill net was lifted.

Studies by the two procedures covered only 3 days, June 17–19, 1954; in 1955, the net method alone was employed (June 2–11). The gizzard shad spawned most actively in the evening and early night in 1954 and at night in 1955 (table 22); spawning was least in the daytime in both years. I have not seen shad spawning during the daytime, but have seen them milling actively, frequently breaking surface, when I lifted the net at midnight, especially in moonlight.

The individuals participating in the spawning change continually during the season, but a female does not deposit all her eggs during one nightly visit to the bar. Although the percentage of eggs remaining in the ovaries varies among individual fish throughout most of the spawning season, numerous partially spent fish with a substantial percentage of eggs still in the ovary are taken early in the season. Almost none carry large percentages of their eggs toward the close of the season. The state of development of the "nearly mature" ova and the free ones in the ovaries of

TABLE 22.—*Shad eggs and the spawning condition of gizzard shad collected during various periods of the day on a spawning site near Put-in-Bay, Ohio, in June 1954 and 1955*

Dates and period of day	Fish taken by gill nets			Eggs on concrete slabs [1]
	Males	Females		
		Not yet spawned	Partly spent	
June 17–19, 1954:	*Number*	*Number*	*Number*	*Number*
6:30 a.m.–7:30 p.m.	0	2	1	2
7:30 p.m.–12 p.m.	91	16	19	15
12 p.m.–6:30 a.m.	50	7	14	5
June 2–11, 1955:				
9 a.m.–4 p.m.	3	0	0	
4 p.m.–12 p.m.	48	4	7	
12 p.m.–9 a.m.	70	6	9	

[1] No observations in 1955.

spawning gizzard shad indicates possible periods of rest between spawnings.

The males captured on the spawning site during the period of most active spawning outnumbered the females three to one. This abundance of males may be attributed to one or more of the following: Their actual daily recruitment to the spawning site, their probable greater activity, or their possible longer stay on the site. I was unable to distinguish any degrees of "spentness" in the male.

Not having observed details of behavior of spawning gizzard shad, I can offer only the statements of others on spawning behavior. Langlois (1954) observed gizzard shad spawning on May 29, 1935, in North Reservoir at Akron, Ohio, near shore in 6 to 12 inches of water at a water temperature of 67° F. During oviposition, a female was flanked by a male on each side. No time of day was indicated. M. B. Trautman (personal communication) observed about 20 shad spawning in Buckeye Lake, Ohio, at 73° F. on May 23, 1939. The females, pursued by several males, swam rapidly toward a sloping stone wall, turned abruptly, and deposited their eggs. A. G. McQuate (personal communication) observed shad spawning in Sandusky Bay, Ohio, on May 24, 1954 (temperature 62.5° F.), along a stony shore near 12 m. (noon) in the shade of an overhanging tree. Female shad were pursued by several males. The fish frequently broke water.

My own failure to see gizzard shad spawning during the daytime at the spawning site in Fishery Bay can be attributed to their failure to spawn at that time. The small daytime catches in gill nets suggest that shad were extremely scarce at the site. I do not believe they avoided the gear, because the nets were treated with a copper preservative that rendered them greenish and, hence, less visible than untreated nets, and were set in aquatic vegetation which almost wholly obscured them. White bass, smallmouth bass, and rock bass, but very few gizzard shad, were caught in the day.

During the midnight lifts, however, when the moon shone brightly, I saw many fish swirling and breaking water. The moonlight was not bright enough for me to judge accurately the species or size. The gill nets caught many gizzard shad, however, during those nights and had many shad eggs adhering to the webbing. The only other fish caught at those times were a few carp.

Hatching and Early Development

The eggs of the gizzard shad are heavier than water and slowly sink after they are spawned. The egg capsules adhere to surfaces that they contact, such as submerged aquatic plants and stones. Experiments in the Ohio State Hatchery at Put-in-Bay indicated that the hatching time varies from about 36 hours to about a week, depending on the temperature. This finding agrees with Warner's [2] observations at Buckeye Lake, Ohio.

In a series of experimental hatchings over 2 seasons, I failed to keep the young alive beyond the 10th day after hatching. Mortality was low up to the 9th day and the fish appeared to be doing well; then suddenly on the 10th day only a few remained alive out of thousands. The remainder died before the day ended. Results were the same in running and aerated water and with various kinds of food, such as natural food from the lake and cultured protozoans.

The movements of the newly hatched gizzard shad were an upward swimming and a downward settling—in each direction the head was foremost. This behavior continued 3–4 days. The whole body moved sinuously with such rapidity that the individual movements could not be followed. At this time the pectoral fins were not yet used to any extent. On the fourth day the fry began to swim horizontally as well as upward and downward. Their mode of swimming at this age,

[2] Warner, E. N. 1940. Studies on the embryology and early life history of the gizzard shad, *Dorosoma cepedianum* LeSueur. Doctoral thesis, Ohio State University. (Unpublished.)

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observed (in a petri dish) under a dissecting microscope, was largely by the pectoral fins which "vibrated" seemingly with the rapidity of the wings of a bee in flight. The sinuous body movement was not abandoned, but the frequency had slowed enough that it could be followed easily.

When food was added to the aquarium, the young shad darted to and fro as though pursuing some of the small particles. Although the digestive tract contained food during the fifth or sixth day, only green algae were recognized through the thin gut wall.

The young shad congregated on the lighted side of the aquarium. If all sides were lighted, they remained mostly near the source of the running water, facing into the current.

The first few days after hatching, the young gizzard shad subsists on its yolk. Increase in length of the 3.5 mm. newly hatched larva at this time results largely from the straightening of the cephalic flexures, after which the larva attains a length slightly greater than 5 mm. About the 5th day it begins to feed and by the 10th day has attained a length of slightly more than 6 mm. (in the laboratory). At this time it has a filiform shape, which it retains until it has reached a length of 20–30 mm. (fish from the lake—age unknown). Upon reaching this length, the shad begins to increase in depth. The filiform shape gives way to the slab-sided, deep-bodied adult form. Once this shape is acquired the form changes little and the shad begins to grow rapidly.

DIGESTIVE TRACT

Development of the Digestive Tract

The gut of a newly hatched gizzard shad is a tube which conforms to the body curvature. In the 10-day-old larva the gut is a simple, nearly straight tube. Among the older shad the gut of an 18-mm. fish (age unknown) had already developed two flexures (fig. 14). The 19-mm. shad had begun the third and fourth flexures, and the 22.5-mm. fry had already completed them. The portion

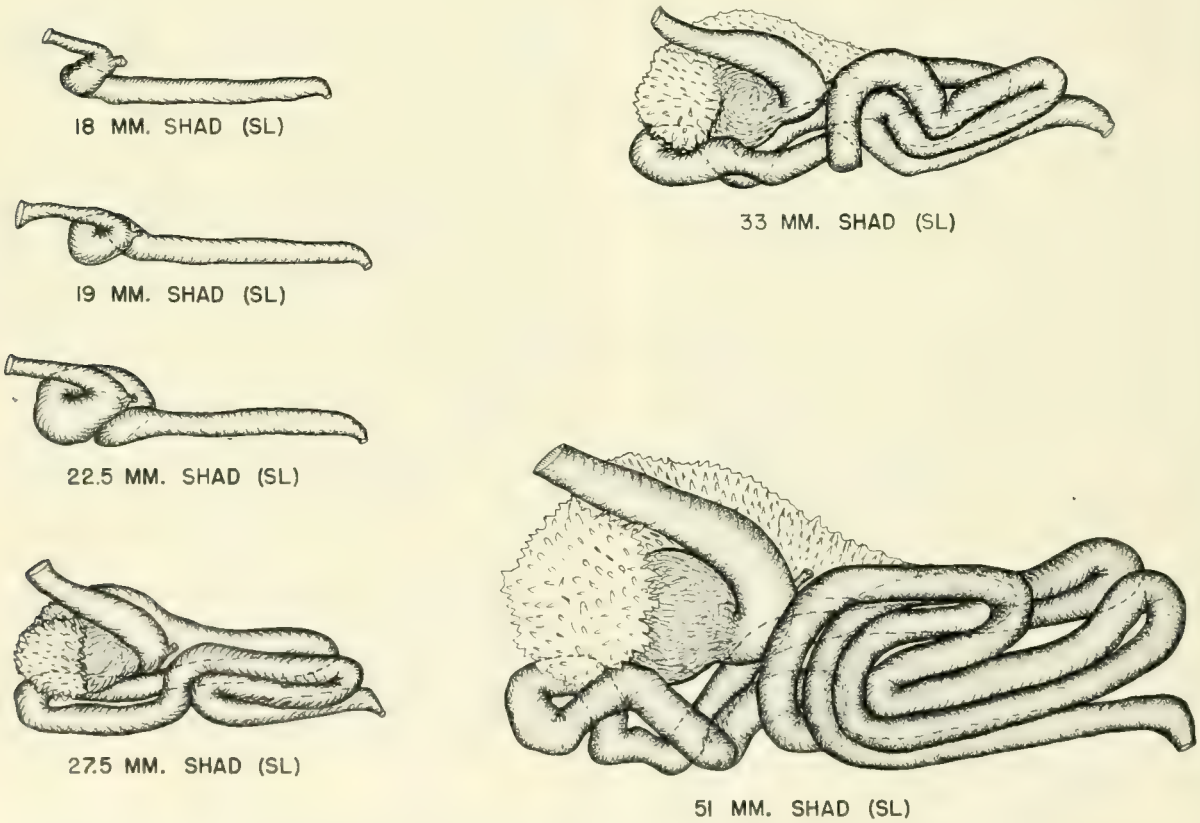

FIGURE 14.—Development of the shad gut (camera lucida drawings).

between the first and second flexures (later to become the gizzard) had enlarged. By the 27.5-mm. stage, the caeca had begun to develop from the duodenum (between the second and third flexures). As the gut continues to grow, the flexures move until they reach the limit of the abdominal cavity. Since the gut grows much faster in length than the abdominal cavity, secondary flexures are produced between the primary ones. Flexures provide landmarks by means of which one can determine relative rates of growth of the different portions of the gut. The caudal portion grows more rapidly and continues to grow over a longer period than any other section. No secondary flexures develop anterior to the third primary one.

Although the course of the gut of a young gizzard shad is complicated, it is relatively simple in comparison with that of the adult of, say, 250 mm., in which the convolutions are so numerous and complex that they defy tracing on a two-dimensional illustration. Indeed, the gut which amounted to one-half of the total length of the day-old fish becomes, in the adult, three times the length of the fish and is packed in an abdominal cavity, one-third of the fish's length.

Forbes (1914) stated that the larva of the gizzard shad has teeth. Although I have examined many young, from newly hatched to longer than 20 mm. (when the adult shape begins to take form), I have not observed teeth.

Digestive Tract in the Adult

The hundreds of long, thin gill rakers of the gizzard shad are admirably adapted for removing particulate matter from the water. This material, especially the filamentous algae and the small crustaceans, apparently is accumulated in the pharyngeal pockets, a paired muscular organ mentioned by Forbes (1888) and described by Lagler and Kraatz (1944). The thick muscular wall and the direct connection with the esophagus suggest that these pharyngeal pouches force their contents into the esophagus. The sphincter muscles in the forepart of the pneumatic duct prevent passage of food into the air bladder.

The muscular esophagus and the gizzard have been described by Wier and Churchill (1945). I can add only that the esophagus possesses longitudinal folds.

Numerous caeca arise in groups on the lateral surface of the duodenum. Each group has a common orifice through which the lumina of its caeca communicate with the lumen of the duodenum. These orifices are arranged in two parallel longitudinal rows. In a 200-mm. shad the lengths of the caeca range from about 5 mm. for those at the anterior end of the row to about 2 mm. at the posterior end. Counts were not made, but an individual appears to possess several hundred caeca. The caeca have internal longitudinal folds. Their lumina are so small that only the smaller unicellular organisms can enter. Although the caeca have the histological appearance of absorptive devices rather than secretory organs, it is only when the duodenum is turgid with food that any material is to be found here.

Wier and Churchill (1945) described a pancreas separate from the liver for the gizzard shad. I have been unable to identify one although I have searched for it repeatedly in many sizes of fish. These authors described the liver as composed of several lobes. I find that it has no definite form in the adult fish but rather seems to spread in close proximity to the gut. The liver invades intercaecal spaces as well as those between neighboring portions of the gut, and completely covers the anterior, dorsal, ventral, and left-lateral surfaces of the gizzard. It is a diffuse organ and intermixed, I believe, with the pancreas.

The small intestine possesses no villi, contrary to the statement of Forbes and Richardson (1908). It does contain four of the large, conspicuous, longitudinal folds described by Wier and Churchill (1945). Attached transversely between the folds and along the inner circumference of the gut are smaller folds or lamellae which have the free edge directed toward the center of the gut lumen (fig. 15). The free edge of each lamella is directed posteriorly at a slight angle. Although the columnar cell covering of these transverse lamellae is unquestionably absorptive and these structures greatly increase the absorptive surface of the gut, they may also function in the manner suggested to me by Milton B. Trautman. He suggested that during peristalsis the longitudinal ridges may lengthen and shorten, thereby causing the lamellae to move back and forth in venetian-blind fashion and, hence, to aid in forcing food along the tract.

This lamellar arrangement within the gut bears some resemblance to the situation described by

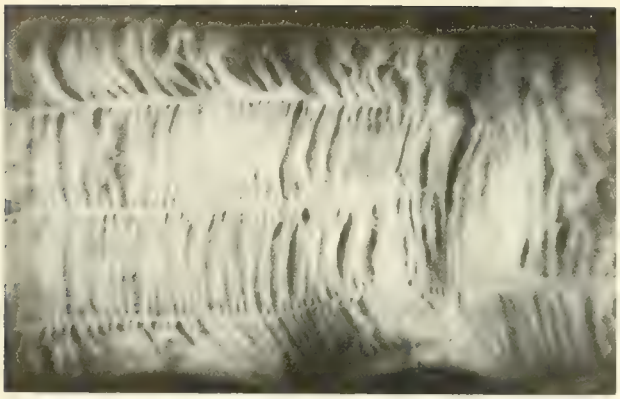

FIGURE 15.—Enlarged view of the small intestine of the gizzard shad showing three of the longitudinal folds with their transverse lamellae.

Kraatz (1924) for the gut of *Campostoma anomalum* in which somewhat similar folds assume a zigzag arrangement.

Transverse lamellae were present in a 22.5-mm. shad. Here they were attached circumferentially to the gut only—the longitudinal folds had not yet formed.

Longitudinal sections of the gut, because they cut across the lamellae, appear to be villous. This fact may account for the statement of Forbes and Richardson that the gut possesses villi.

Digestive Enzymes

Only a qualitative study was made of the digestive enzymes. Attempts to determine their quantity or potency did not yield dependably accurate results. The areas tested were: Pharyngeal pockets, esophagus, gizzard, duodenum (that forepart of the gut bearing the caeca), hepatopancreas, gall bladder, and the first, second, and third portions of the intestine. The materials were prepared in the usual manner and the extraction made with 50 percent glycerol.

Tests were made for the following enzymes: Pepsin, trypsin, amylase, lipase, maltase, sucrase, and rennin. In addition, I sought enzymes that would act on chitin and cellulose.

The enzyme giving the strongest reaction was amylase (table 23). It was present in all areas tested. The reactions for pepsin and trypsin were moderate, whereas the reaction for lipase was weak. I am at a loss to explain the significance of the positive test for rennin.

The presence of enzymes in the esophagus is not restricted to the gizzard shad. Sarbahi (1951) found amylase, maltase, and invertase in the esophagus of the goldfish, and Kenyon (1925) cited Kingsley as reporting gastric glands in the esophagus of the sturgeon.

FOOD AND FEEDING HABITS

The young gizzard shad begins to feed about 4 or 5 days after hatching. The earliest food is probably Protozoa and unicellular algae. When the shad has attained a length of about 20 mm., it feeds on the smaller of the zooplankters and takes practically no phytoplankton. By the time it is 30 mm. long it has assumed the adult shape, and its gizzard is fairly well developed. The fish now begins to feed more and more on phytoplankton.

Three opinions have been offered in the literature regarding the nature of the food of adult gizzard shad. Some believe they eat predominately mud; others insist that they feed almost wholly on

TABLE 23.—*Digestive enzymes found in the gizzard shad*

[If no value is given, a test was not made. The numerical ratings are: 0, negative; 1, not definite; 2, perceptible; 3, small; 4, considerable; 5, strong]

Enzyme	Area tested								
	Pharyngeal pockets	Esophagus	Gizzard	Duodenum	Intestine			Hepato-pancreas	Gall bladder
					1st part	2d part	3d part		
Pepsin	0	3	4	3	0	0	0	2	0
Trypsin	0		0	4				3	2
Amylase	3	3	3	4	4	4	3	5	4
Lipase	0	0	1	2	0	0	0	3	2
Maltase	0	0	0	1	0	0	0	1	1
Sucrase	0	0	0	2	0	0	0	0	0
Rennin	0	0	1	3				3	0
"Chitinase"	0	0	0	0	0	0	0	0	0
"Cellulase"	0	0	0	0	0	0	0	0	0

TABLE 24.—*Monthly record of occurrence of various items in stomach contents of gizzard shad in 1952-55*

Month	Material in digestive tract											
	Debris	Sand	Diatoms	Dinoflagellates	Blue-green algae	Green algae	Protozoans	Rotifers	Ostracods	Copepods	Cladocerans	Insect larvae
Jan.	X											
Feb.	X											
Mar.	X											
Apr.	*X	X	X			X		X				
May	*X	X	X			X				X		
June	*X	*X	*X			*X	X	*X		*X	*X	X
July	X	*X	*X	X	*X	*X	X	*X	X	*X	*X	X
Aug.	X	*X	*X	X	*X	*X	X	*X	X	*X	*X	X
Sept.	X	X	X		X	*X		X		X	X	
Oct.	X	X	*X			*X		X			X	X
Nov.	X		*X			*X		X		X	X	
Dec.	X											

*Indicates the more plentiful items.

phytoplankton; still others maintain that they subsist mostly on zooplankton. All agree, however, that they are "filter-feeders," and this feature alone, I believe, best describes their feeding habits. They filter the water of whatever particulate matter it contains. Shad captured in open waters contained mostly free-floating phytoplankton; those captured among the attached plants, such as *Cladophora*, *Myriophyllum*, and *Ceratophyllum*, ingested Cladocera, Copepoda, Rotifera, and small aquatic insect larvae; those captured in very turbid waters were filled largely with mud. That they do, however, add to their diet from the bottom debris is evidenced by the presence in the gizzard of sand particles of diameters in excess of 0.25 mm. This size of sand is not held in suspension even when the water is highly turbid. Although the bottom is available to the shad at all times, I have not found sand in shad gizzards from December through March. Food particles could not be identified during this period. The taking of sand when food is plentiful suggests its use as an aid in grinding by the gizzard—or it may have been taken accidentally along with food.

The appearance of the food differs in the three distinct regions of the alimentary apparatus—the pharyngeal pockets, the gizzard, and the intestine (especially the forepart which bears caeca and which is often swollen with ingested material). When reference is made to food in the gizzard shad without regard to a definite region of the digestive tract, I use the term "stomach contents."

The pharyngeal pockets, suggested by Lagler and Kraatz (1944) to be accessory to the digestive system, have, to my knowledge, not been thoroughly examined in studies of food of gizzard shad. The pouches frequently are empty, but when food is plentiful and the fish's gut is full of food (especially zooplankton), the pharyngeal pockets contain as much food as the gizzard. The contents of these pockets appear straw-colored and consist mostly of Cladocera and Copepoda along with strands of filamentous algae. Here are found the larger items of the shad's diet, and they are, as yet, not broken apart. The zooplankters still have their full complement of appendages and the filamentous algae are in strands.

The gizzard is frequently empty, and only rarely is it turgid with food. The composition of food in the gizzard is similar to that of the pharyngeal pockets. The zooplankters, however, are more or less dismembered, and the strands of filamentous algae are short. The gizzard contains, in addition, many unicellular algae, rotifers, and some sand along with plant and animal debris.

The intestine usually contains food, although the amount is scanty in winter. Material from the intestine is fragmented and mostly unrecognizable—it has the appearance of bottom debris or mud, especially on gross inspection.

I have found no compact matter exceeding a diameter of 3 mm. in the stomach contents of gizzard shad, except Tendipedidae and small *Leptodora* during certain seasons. Nor have I found in them bits of attached aquatic plants, except after severe storms when small fragments were presumably torn loose and were recovered by the filtering apparatus.

The stomach contents of adult gizzard shad exhibited no appreciable differences among individual shad of a group collected in a locality at the same time. Evidence was lacking for any selection of food within the size range of material they swallow. There were, however, local and seasonal differences related, undoubtedly, to the abundance of the various forms in different places and at different times. As a result of these observations, examination of stomachs of individual fish was soon discontinued and the stomach contents of several fish of a collection were combined.

The feeding habits of gizzard shad were well summarized by Tiffany (1920) who indicated them to be a living tow net. No attempt was made in the present study either to obtain the percentage of each item ingested or to enumerate every organism eaten by the shad at one time or another. In table 24 are listed only major groups of materials found in shad during various months. The table does not identify the months in which the gut contained the most food; in general, the quantity was more plentiful when the diet consisted of a great variety of food in June through November.

Velasquez (1939) cultured algae taken from various parts of the shad gut. As a result either of rapid transit through the gut, or absence of certain enzymes, some algae or certain algae apparently are not utilized as food.

SUMMARY

This study of the life history of the gizzard shad was based on records of the length, weight, and age of almost 24,000 specimens taken in western Lake Erie in 1952–55. Approximate numbers of fish employed in other phases of the study were: calculation of growth from scale measurements, 700; seasonal fluctuations of gonad weight, 700; sex ratio and maturity, almost all fish over 120 mm. long; feeding habits, 200; seasonal development of ovaries, 150; and fecundity, 13.

The fish were captured by means of dip nets, "Common Sense" seines, bag seines, push seine, gill nets of various mesh sizes, regulation commercial trap nets, and by electric shock, dynamite, and rotenone. Fish older than the O-group were captured mostly by the gill nets and trap nets. Most fish were captured within one-half of a mile of the Bass Islands.

The scales of the gizzard shad are described briefly. Two types of annuli are present—a narrow clear-cut line of demarcation and a wider, more evident one. The first annulus is always of the former variety; the second and succeeding ones (with few exceptions) are of the latter variety. The wider, obvious annulus may be a combination of an annulus and a spawning check, while the narrow variety is strictly an annulus.

The time of annulus formation varied with age and sex. Some of the I-group shad began to form the new annulus in May, and all had it by the end of the first quarter of June. Annulus formation of older shad began in June and was completed by mid-July. Females seem to have formed their new annulus about a week earlier than the males. Spawning of these older females occurred while annulus formation was in progress—some fish spawned before the appearance of the new annulus—some after its appearance. Although prespawning development of the gonads was thought to affect the physical appearance of the annulus, the spawning act appeared to have no effect on the time of its appearance. Evidence was given that the annulus is a true year mark.

The body-scale relation was a straight line with an intercept of 22.1 mm. on the axis of standard length.

Calculated lengths showed good agreement with empirical lengths of shad captured between the first of the year and the time of annulus formation—except for the I group. The greater average length of I-group fish at capture can be attributed to gear selectivity.

Sampling problems made the determination of age composition difficult. The young gizzard shad were found in shallow water, the older in deeper water, and the very oldest were captured only during the spawning season. Shad captured in the open lake during fall probably gave the best available estimate of the relative strength of younger age groups. Those captured during the spawning season were most nearly representative of the age composition among the older shad. On these assumptions the following survival from an original 100,000 I-group fish were computed: II-group, 5,534; III-group, 435; IV-group, 63; V-group, 11; and VI-group, 6.

The 1952 year class was one of more than usual abundance. In 1953, as I-group they constituted

85 percent of the fish caught; in 1954, 71 percent as II-group; and in 1955, 11 percent as III-group.

Males made up 45.6 to 49.7 percent of the fish in the four younger age groups (O–III). They were less abundant (36.6 percent) in the age groups IV–VI combined. During the spawning season the percentage of males on the inshore spawning site was greater than normal but that in the open lake was less.

The length-weight relation of gizzard shad varies from year to year, from season to season within the year, according to sex during the spawning season, and among the females according to the state of the ovaries during the spawning season.

Equations were derived for length-weight data and from them was obtained the general length-weight equation, $\log W = -4.81765 + 3.07053 \log L$, in which W is the weight in grams and L the standard length in mm. Gizzard shad from Lake Erie were heavier than those reported from Illinois and Missouri.

Fish of the same length had the greatest weight in August–October. Males were lightest in June; females in May. The spawning-season female was heavier than the male; this difference in weight was not traceable to the gonadal development in the female, but may result from the greater activity of the male at this period. Among the females in the spawning season, those which would not spawn during the current season were the heaviest, those approaching spawning were next, and spent fish were the lightest. The percentage loss in weight during spawning averaged 10.7.

Annual differences in shad weight from relatively heaviest to lightest ran: 1952, 1954, 1955, 1953.

Most of the growth in length for the O-group (which hatched in June) occurred in July–September; for the I-group during June–August; and for the II-group during July–September. Gizzard shad of the II-group and older commence their rapid growth in length about a month later than the I-group fish. Shad lengths remain practically stationary from November until the time of annulus formation.

Males and females had almost the same length at the end of the first year (140 mm.) but after about June of the second year of life the females were consistently longer than males of corresponding ages. The sizes of males and females at the start of different growing seasons were: third, males, 273 mm. and females, 285 mm.; fourth, males, 313 mm. and females, 335 mm.; fifth, males, 343 mm. and females, 364 mm.; sixth, males, 349 mm. and females, 386 mm.

The seasonal growth in weight resembles that of the growth in length except that weight decreases during winter while length remains nearly constant. This loss of weight begins about the start of the year and continues until about May.

Differences among the lengths of individuals of an age group at the end of a calendar year tend to be reduced by later compensatory growth. At the end of succeeding years those fish that were the longest of their year class maintain a length advantage, but this advantage decreases.

The stage of egg development varied from fish to fish throughout most of the year, but with the approach of the spawning season, the retarded shad increased their pace of development while the advanced ones slowed down so that the condition of the ovaries became much more nearly uniform.

A brief description is given of the testis and of various stages of the ovary. The developing egg and the seasonal changes in the saccular ovary also are described.

Not all mature eggs are expelled at the same time. Eggs which are not mature are held over for next year, and those which develop to the spawning stage too late to be expelled are resorbed.

Only rarely were I-group female shad ripe. Most of them (an estimated 80 percent) spawn for the first time as II-group fish. The age of sexual maturity could not be determined for the male; males examined in January had motile sperm—even the new I group. The number of II-group males on the spawning site suggests that most mature as the II-group—the few I-group individuals present may be termed precocious.

A spawning site in the vicinity of Fishery Bay, South Bass Island, was a sandy, rocky bar covered with 2–4 feet of water. Gizzard shad were captured here only during the spawning season—almost all during the evening and night. Spawning was limited in the open lake. The females that are ready to spawn migrate to inshore spawning sites. After spawning, they return to the deeper water. Males also migrate to the spawning sites where they are two or three times

as numerous as the females. The representation of the sexes was nearly equal in the open lake at this time. Spawning was most active in the evening and early night in 1954 and in the night in 1955.

Spawning occurred from the first quarter of June through the first quarter of July; peak spawning was in the second quarter of June. The precociously mature I-group fish spawn in late July or later.

The II-group shad produce the greatest number of eggs—about 379,000. In decreasing order are: III-group, 345,000; IV-group, 309,000; VI-group, 215,000; and the precocious fishes of the I-group, 59,000.

On the basis of eggs per gram of fish, relative fecundity triples from age group I to II and then declines to age group VI, which has about the same value as the I group.

The eggs of the shad hatch in 1½ to 7 days, depending on the temperature. The movements of young fry are described.

The gut of a small larva is a nearly straight tube. Sometime after the 10th day the gut begins to fold. The convolutions become more and more complex with increasing size. The gizzard becomes evident in the 22.5-mm. stage. The liver is a diffuse organ, apparently mixed with the pancreas; no pancreas was found.

The intestine lacks villi but has longitudinal folds and transverse lamellae which increase the absorptive surface and may help move the food along during peristalsis.

The presence of sand in the gut when ingested food is plentiful and its absence in winter, when the gut is empty, suggest that it may be taken as an aid in grinding the food in the gizzard.

Food was frequently present in the pharyngeal pockets of large gizzard shad whose gizzard and intestine were packed with food. The presence here of long strands of filamentous algae, and Cladocera and Copepoda with their full complement of appendages, repudiates statements that they are regurgitated into the pockets. In the gizzard, these items were always in some stage of dismemberment.

Tests were positive for the following digestive enzymes: pepsin, trypsin, amylase, lipase, and rennin. Amylase was found in all areas of the tract.

The earliest food of gizzard shad appears to be Protozoa. At a length of about 20 mm., shad feed almost wholly on the smaller of the zooplankters. After the 30-mm. stage, the digestive tract contains greater and greater percentages of phytoplankters. "Filter feeders" best describes the habits of adults. Zooplankters or phytoplankters may predominate in the gut according to their abundance in the water in which the fish are feeding. By the time the food reaches the intestine it has been macerated and partially digested so that it resembles mud. This fact may explain the frequent statement that shad eat mud.

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BIOACCUMULATION OF RADIOACTIVE GOLD USED AS A SEDIMENT TRACER IN THE ESTUARINE ENVIRONMENT [1]

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ABSTRACT

The accumulation of radioactive gold by selected members of a marine animal community and sediment material was followed under laboratory and field conditions. In the laboratory an aqueous solution of radioactive gold was placed directly in the gut of blue crabs, toadfish, and croakers. There was little transfer of the isotope to various tissues in these organisms. A group of toadfish which were fed radioactive gold in an aqueous solution retained more of the isotope than did a group which were fed the same amount of radioactivity sorbed onto clay particles. Also, crabs, fish, clams, and samples of bentonite clay were maintained for 25 days in 1,000 liters of cotton-filtered sea water containing radioactive gold. Crabs accumulated the most radioactivity followed, in descending order, by clams, clay, and fish. A field experiment was conducted in cooperation with the U.S. Army Corps of Engineers in the Cape Fear River, N.C. Caged and indigenous free-swimming organisms were exposed to sediment-sorbed radioactive gold used as a sediment tracer by the Corps. Oysters, crabs, and fish maintained in cages in the experimental area were sampled periodically. The maximum level of radioactive gold in the caged organisms (70.9 millimicrocuries per gram wet weight tissue) was detected in oysters 17 hours after the isotope was released. Indigenous organisms collected 41 hours after the radioactivity was released contained no detectable radioactive gold.

The uncontrolled release of radioactivity into estuarine waters could so contaminate marine organisms that they would be unsafe for use as food by man. However, with the use of basic data from laboratory experiments to evaluate the quantity and rates of release of radioactive materials, and with sensitive instruments to measure the resulting levels of radioactivity, radioisotopes can be released into the natural environment without adversely affecting seafood organisms. Also, when released in this manner, radioisotopes can safely be used *in situ* to investigate many ecological problems.

A study was made to determine the bioaccumulation of sediment-sorbed radioactive gold released into the Cape Fear River. This study was carried out with investigators of the U.S. Army Corps of Engineers, who used this isotope to trace sediment movement in the river. Prior to this investigation, radioactive gold had been used successfully as a sediment tracer by the Corps of Engineers in several bays and harbor systems in the United States.

Determinations of gold in marine organisms have been reported by Noddack (1939), Vinogradov (1944), and more recently by Fukai (1962). Equilibrium values for the distribution of gold between sea water and organisms have been calculated by Krone (1959) using the data of both Noddack and Vinogradov. The capacity of marine organisms to accumulate radioactive gold from contaminated sea water or from contaminated food organisms has not been determined.

Since marine organisms could be exposed to radioactive gold used in sediment tracer experiments, an evaluation of the accumulation of this isotope by several marine organisms was made by (1) conducting laboratory experiments to deter-

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mine the behavior of gold in sea water, and the translocation of this element in several animals; (2) observing the transfer of radioactive gold from sea water to a community maintained in a large salt-water tank; and (3) measuring the accumulation of the isotope in animals and sediments in the natural environment.

PRELIMINARY LABORATORY EXPERIMENTS

The behavior of radioactive gold in sea water, its affinity for sediments, and its assimilation by individual organisms were studied prior to following the movement of radioactive gold through a community of organisms. Characteristics of radioactive gold in sea water and the effect of salinity on the sediment-sorption of this isotope were observed. Bentonite clay composed of montmorillonite clay minerals was used in the sediment-sorption experiments because of the natural occurrence of these minerals in marine sediments and because of their reported sorptive properties (Grim, 1953). Experiments on the assimilation of radioactive gold by individual animals were conducted in sea water ranging in salinity from 28 to 32 °/₀₀ and having a temperature range of 27.0° to 30.2° C. These animals included blue crabs, *Callinectes sapidus;* oyster toadfish, *Opsanus tau;* and Atlantic croakers, *Micropogon undulatus;* all collected near Beaufort, N.C.

Gold 199 was selected in preference to gold 198 because of its longer half-life (3.1 days compared with 2.7 days) and its availability in the carrier-free form (2.09×10^5 curies (c.)/gram). The gold 199 in the form of auric chloride was supplied from Oak Ridge, Tenn.

The radioactivity content of sediment, water, and animals in these preliminary experiments was measured with a scintillation detector large enough to contain live animals (4¼ inches diameter by 9 inches long) and a single-channel gamma spectrometer. Measurements were corrected for decay, geometry, and background.

BEHAVIOR OF RADIOACTIVE GOLD IN SEA WATER

The behavior of tracer amounts of radioactive gold in aqueous solutions was investigated by Schweitzer and Bishop (1953). These investigators have shown by filtration and centrifugation that gold (in concentrations less than 10^{-8} M) appears to behave as a radiocolloid in certain aqueous solutions ranging in pH from 2 to 12. Schweitzer and Jackson (1952) also discussed the use of cation exchangers in the identification of radiocolloids. The uptake of a cationic tracer by an exchanger should decrease with an increase in the cationic concentration of the solution. If the tracer is a radiocolloid, however, the uptake increases as the cationic concentration increases. This is attributed to the effects of the cations acting as a coagulant and the exchanger acting as an absorbent.

Several experiments were conducted in this study to determine, qualitatively, the behavior of radioactive gold in sea water. A water sample was prepared by adding 200 microcuries (μc.) of gold 199 (4.9×10^{-11} M) to 1 liter of Millipore-filtered sea water of 30 °/₀₀ salinity and a pH of 8.2. The temperature of the water was maintained at 25°±2° C. during the experiment. Centrifugation of 500 ml. of this sample at 3,000 r.p.m. for 15 minutes forced 58 percent of the radioactivity to the bottom of the tube indicating that gold particles had been formed. When 500 ml. of the initial sample were passed through a Millipore filter of 45 millimicrons (mμ) pore diameter, 100 percent of the radioactivity was removed. Even though some of the gold could have been retained as a result of pores being clogged by large molecules, the gold in sea water appeared to be particulate, rather than ionic.

Further indications of the properties of radioactive gold in sea water were obtained by observing the sorption of gold onto clay. Equal amounts (200 μc.) of gold 199 were placed in four tanks, each containing 1 liter of millipore-filtered water and 1 g. of clay. The first tank contained distilled water; the second, water having a salinity of 8°/₀₀; the third, 24°/₀₀; and the fourth, 34°/₀₀. The waters having salinities of 8°/₀₀ and 24°/₀₀ were prepared by adding appropriate amounts of distilled water to sea water having a salinity of 34°/₀₀. The water in the tanks was agitated for 15 minutes and allowed to stand for 24 hours. The clay slurry was withdrawn from each tank, centrifuged, and the water decanted. The clay was then dried and the amount of radioactive gold measured.

The uptake of gold 199 on clay increased as the salinity increased (fig. 1). There are at least two possible explanations for this sorption phe-

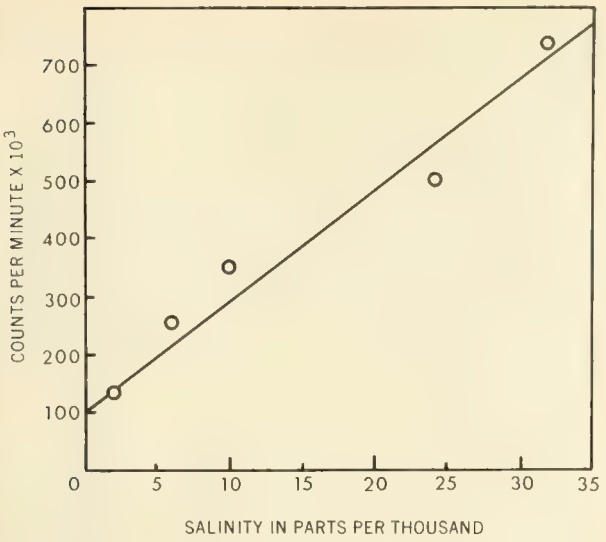

FIGURE 1.—Sorption of gold 199 by montmorillonite clay from sea water with increasing salinity.

nomenon: (1) An increase in salinity caused the clay to clump, and radioactive gold was trapped within the clumps; and (2) The increase in salinity caused the gold particles to coagulate and to sorb more readily onto the clay. If the latter explanation is accepted as correct, it would appear that radioactive gold was colloidal in this sample of sea water.

DISTRIBUTION OF RADIOACTIVE GOLD IN BLUE CRABS

Edible portions of an organism such as a blue crab can be relatively free from radioactivity even though the total radioactivity content of the organism is high. This is possible when the activity is isolated in the stomach or associated with the highly sorptive carapace and other external sites. That this does occur was shown by determining the distribution of ingested radioactive gold in the blue crab. Twelve crabs with an average weight of 152 g. were made radioactive by pipetting 75.7 μc. (50 microliters) of gold 199 directly into the cardiac stomach of each crab. They were then placed in flowing sea water. At intervals of 3, 4, and 5 days after dosing, three crabs were killed, dissected, and measured for contained activity.

Radioactivity content of tissues at 4 days indicated that only a small portion of the gold 199 was assimilated from the stomach (table 1). In view of the short half-life of the isotope, more than tracer amounts of radioactive gold would need to be ingested rapidly in order to build up concentrations in edible tissues.

DISTRIBUTION OF RADIOACTIVE GOLD IN TOADFISH

Bottom feeders, such as the oyster toadfish, could become radioactive by taking in sediments with loosely bound sorbed activity. If the radioactivity were tightly bound to the sediment particles, however, the sediment-sorption phenomenon would reduce the possibility of animal contamination by retaining and confining the radioactivity.

TABLE 1.—*Radioactivity content of crab tissue 4 days after an oral dose of 75.7 μc. of gold 199*

Tissue	Activity	Dose in entire tissue
	μc./g.	*Percent*
Digestive gland	9.3×10^{-1}	12
Stomach—gut	8.4×10^{-1}	3
Gonad	1.6×10^{-1}	.8
Gills	5.3×10^{-2}	.7
Muscle	2.5×10^{-2}	.6
Carapace	3.8×10^{-3}	.08
Blood	1.7×10^{-3}	.04
Total		17

To test the capacity of fish to "strip" radioactive material from sediments, five male toadfish, average weight 325 g., were each force-fed 75.7 μc. of radioactive gold dispersed in 2 ml. of sea water. Five other males of similar size were fed the same amount of radioactivity sorbed onto 25 mg. of montmorillonite clay suspended in 2 ml. of sea water. The sea water used in both instances had a salinity of 30‰ and a pH of 8.1. After the fish had been fed the isotope, they were placed in flowing sea water. Forty-eight hours later, the fish were killed and dissected, and the amount of radioactive gold in various tissues was measured.

A comparison of the activity of tissues from both groups of fish shows that most of the gold remained sorbed onto the clay as it passed through the digestive system of the fish (table 2). The fish fed the isotope in sea water retained more activity than those fed the isotope sorbed onto clay.

DISTRIBUTION OF RADIOACTIVE GOLD IN CROAKERS

The gastro-intestinal absorption and distribution of gold 199 in the tissues of the croaker were determined after 75.7 μc. of the isotope were

TABLE 2.—*Radioactivity content of toadfish tissues following oral doses of gold 199*

Tissue	Gold administered in solution	Gold administered sorbed onto sediment
	μc./g.	*μc./g.*
Stomach	3.6×10^{-1}	6×10^{-3}
Liver	1.5×10^{-1}	8×10^{-4}
Gut	1.1×10^{-1}	5×10^{-2}
Gill	4.3×10^{-2}	2×10^{-4}
Kidney	4.0×10^{-3}	1×10^{-3}
Blood	4.0×10^{-3}	5×10^{-4}

pipetted into the stomachs of six fish. The fish were then placed in flowing sea water. Three were killed, dissected, and tissues were measured for radioactive gold content after 78 hours and three after 148 hours.

Less than 1 percent of the dose was assimilated by the tissue, about 99 percent having been eliminated within 78 hours (table 3). Of the relatively small amount assimilated, kidney and gills had the highest concentrations of gold 199 per unit weight. After 148 hours the gills and spleen had the highest concentrations. The increase in gold 199 content in some of the tissues during the period from 78 to 148 hours is probably the result of continued assimilation from the digestive tract and translocation of gold 199 from other tissues.

TABLE 3.—*Distribution of radioactive gold in croaker tissue*

Tissue	Dose	
	78 hours	148 hours
	Percent	*Percent*
Kidney	0.038	0.01
Gills	.035	.056
Skin, scales	.017	.009
Liver	.006	.02
Muscle	.003	.03
Heart	.002	.0008
Spleen	.001	.042
Gonad		.001

EXPERIMENTAL ENVIRONMENT STUDY

Since the planned application of radioactive gold in the Cape Fear River would expose the community of indigenous organisms further laboratory studies were conducted with a marine community maintained in a large tank. Data obtained from tank experiments involving relatively large volumes of sea water (1,000 l.) and a community of organisms have advantages over data for individual species held in smaller volumes of water. Increasing the volume of water enlarges the experimental environment, and chronic as well as acute contamination can be observed since observations can be made over longer periods of time because of the improved physiological condition of the organism.

An experimental environment was established to follow the movement of radioactive gold in a marine community. The community, which consisted of clams and clam shells, *Mercenaria mercenaria*; blue crabs; and sheepshead minnow, *Cyprinodon variegatus*; as well as sediment samples of clay, was installed in a large (172 by 117 by 61 cm.) fiberglass tank containing 1,000 l. of cotton-filtered sea water (table 4). Ten clams were placed directly on the bottom of the tank, and 10 in the sediment. Enough gold 199, as $AuCl_3$, was added to the water to give a concentration of 0.0142 μc/ml. After the gold was added, the pH of the water was 8.1. Throughout the experiment the water temperature was maintained at 21°± 3° C. and the salinity at $32\pm0.10‰$, the latter by adding distilled water when necessary to compensate for evaporation. A plastic impeller pump circulated the water continuously.

Clay sediment introduced into the tank was first placed in glass bowls (3 cm. deep by 12.7 cm. in diameter) after being thoroughly wetted as follows: 6 kg. of clay were suspended in 10 liters of sea water for 48 hours, and the excess water was decanted from the clay, leaving it with a pastelike consistency. In each bowl, 200 g. of the wet clay (125 g. dry weight) were placed forming a smooth substrate that was not disturbed by water circulation.

The radioactivity content of whole animals and sediment was measured periodically, with the organisms afterward being returned to the tank. Oysters, clams, and crabs were prepared for radioactivity analysis by wrapping them in a thin transparent plastic sheet. Fish were placed in dark glass jars containing nonradioactive sea water and counted for 3 minutes. Sediments were removed from the tank with a small diameter (2.5 cm.) core sampler and were not returned to the tank. This procedure of measuring the activity in a whole animal eliminated the need for killing it, and the number of individuals was not reduced with sampling. Also, uptake could be followed on the same individual throughout the experiment.

Appropriate corrections were made for decay, geometry, and background on all radioactivity measurements unless otherwise stated.

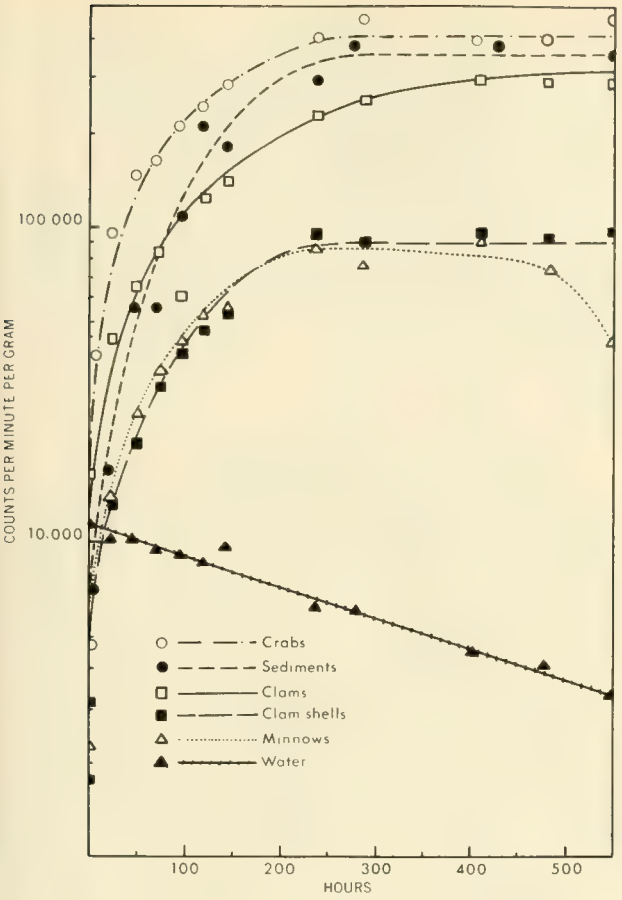

FIGURE 2.—Movement of gold 199 in an experimental marine environment.

Components of the community rapidly accumulated radioactive gold and reached an apparent steady state after 225 hours (fig. 2). There was not a direct relation between the accumulation of the radioactive gold by the components and the loss of the isotope from the water. Even though the radioactive content of the organisms and sediments did not increase after 225 hours, the radioactivity content of the water continued to decrease. This decrease was attributed to sorption of the radioactivity to exposed surfaces in the tank (a total area of 29,784 cm.^{2}) and to accumulation by patches of bacterial film that appeared on the sides of the tank after the experiment had been in progress about 120 hours. Although it was not possible to measure the total amount of film present, 1 g. of this material contained 57 μc. of radioactive gold after 600 hours. The distribution of the radioactive gold in the community at the end of the experiment is shown in table 4.

TABLE 4.—*Composition of experimental environment showing distribution of gold 199, 600 hours after introduction of the isotope*

Component	Individuals	Total wet weight	Gold 199 content after 600 hours
	Number	*G.*	*μc.*
Water		1.0×10^6	4,600
Sediment		1,000	330
Crabs	5	620	340
Clams	20	2,800	1,100
Clam shells	10	130	10
Fish	10	46	230
Total uptake by components			6,610
Loss unaccounted for			7,590

Crabs accumulated more radioactive gold than the other organisms in the experiment. As an estuarine species, blue crabs are a part of a marine community that appears most likely to be exposed to radioactive material in any appreciable concentration. As bottom-dwelling, omnivorous predators and scavengers, blue crabs are, at one time or another, in contact with almost all of the abiotic components of their environment. The carapace and gills offer many surface sites for sorption of materials from the environment. Gill area alone of a blue crab has been estimated to be about 275,000 mm.^{2} (Gray, 1957).

Although sediments often are not included in the food web of marine organisms, many organisms can utilize materials sorbed onto sediments as a source of nourishment. Thus, it is necessary to observe accumulation of gold by sediments as well

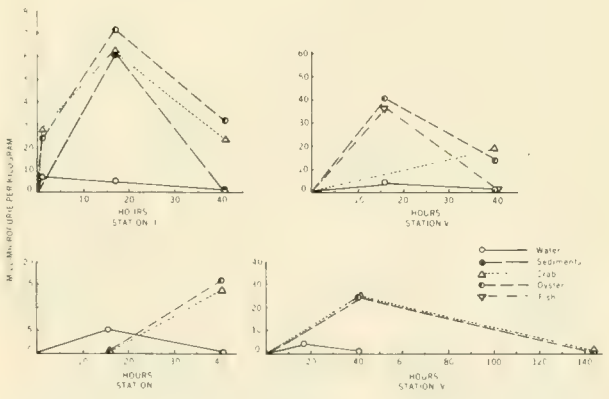

FIGURE 3.—Sorption of gold 199 by sediment in an experimental environment. Curve *A* is activity corrected for decay, curve *B* is observed activity.

as accumulation by the biota. In the present experiment, an increase in sediment activity up to the 250th hour occurred (figs. 2 and 3). From this time until the experiment ended, the activity was maintained with no significant increase or loss; it appears that the sediments were saturated with gold at 250 hours (curve A, fig. 3). The actual activity of the sediments, uncorrected for decay, is shown in curve B of figure 3. The latter values would be of more importance to the health physicists, as they show the actual amount of activity present in the sediments. If the gold were released into sea water in a restricted area where dispersion was minimal, these results indicate that natural decay would exceed uptake after about 150 hours with a resulting decrease in sediment activity.

Live clams accumulated more radioactivity than did the separated clam shells. Since clams feed by filtering suspended matter from large volumes of water passing over their gills, they are susceptible to contamination from particulate radioactive materials released into the estuarine environment. As bottom dwellers, restricted in their movements, they are in contact with sediments and associated radionuclides. A comparison of the mean radioactivity content of 10 clams to 10 separated clam shells on a unit weight basis by a standard t test at the .05 level showed that live clams were significantly more radioactive. The higher concentration of the isotope in the live animals was attributed to the movement of water through the animals. This movement would expose internal tissues as well as shell surfaces to contaminated water.

The clams placed on top of the sediment at the beginning of the experiment accumulated much less radioactive gold than those placed in areas without sediment. As the experiment progressed, the clams burrowed into the sediments, leaving only a portion of their shells exposed. The burrowing clams contained 38 percent less activity than those that remained on the bottom surface of the tank—an indication that a large portion of the gold accumulated by clams was due to sorption of the shell.

Fish accumulate radioactive materials by adsorption, absorption, or by ingestion. In nature, these three modes of uptake can occur simultaneously, singly, or in various combinations, depending upon the physical state of the isotope in the water, the food habits of the fish, and the length of time the fish remains in a polluted area. In this experiment, the sheepshead minnow accumulated the least amount of radioactive gold of any test organisms (fig. 2). The activity of the fish decreased during the latter stages of the experiment. A sloughing off of the epidermal mucous layer containing sorbed activity could account for the loss, or the physiological condition of the fish could have deteriorated and their rate of metabolism changed.

FIELD INVESTIGATIONS

The accumulation of radioactive gold released into the Cape Fear River was observed in both indigenous organisms and in caged organisms collected in Beaufort and maintained in the river. The investigations were coordinated with the release of radioactive gold which had been sorbed onto sediment particles.

The specific problem under investigation by the U.S. Army Corps of Engineers was to determine if sediment being deposited in the channels of the Cape Fear River, N.C., near the Sunny Point Army Piers near Southport, N.C., had been transported by currents from a spoil area on the opposite side of the river (U.S. Army Corps of Engineers, 1964). The answer was sought by tagging a small quantity of the sediment with gold 198, releasing this sediment in the spoil area, and tracing its distribution with an underwater scintillation probe mounted on a sled. The sediment was tagged by first forming a slurry into which 5 c. of gold 198 chloride were thoroughly mixed to allow maximum sorption. This was done in a special conical-bottomed container which served also as the release mechanism for the tagged sediment. The container floated in the water and was towed by boat over a predetermined course while the tagged sediment was being released. The entire procedure has been described in greater detail by Krone (1960).

Gold-tagged sediments were released at two different sites. The first 5 c. "drop" was made on October 24, 1962, at 6 p.m., at high tide, along an east-west line on the southern end of the Spoil area (fig. 4). A second 5 c. drop was made on the northern end of the spoil area on October 25 at 4 p.m., also at high tide. A water sample collected in the drop zone at this time had a

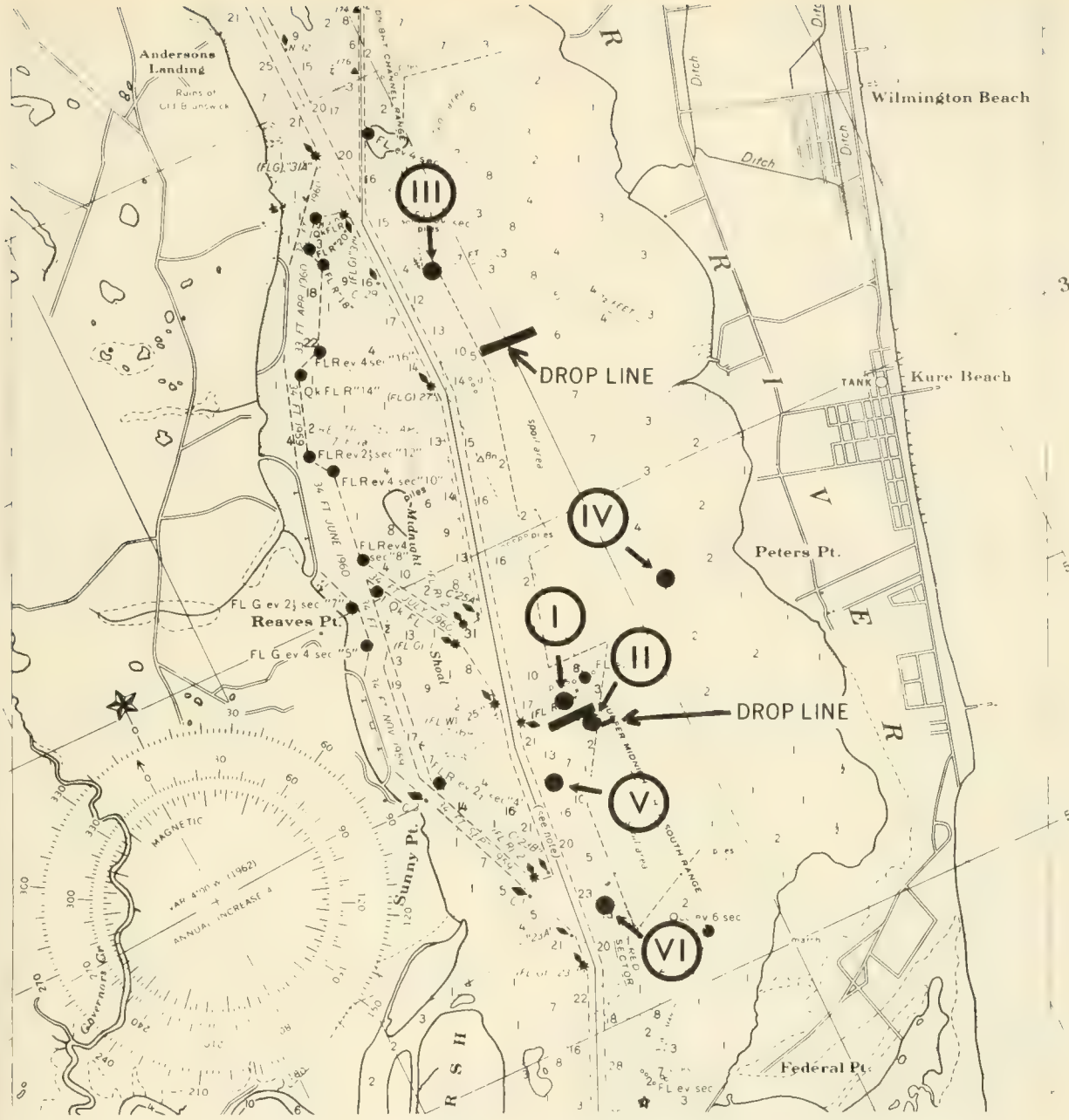

FIGURE 4.—Location of sampling stations and gold tracer drop zones in the Cape Fear River.

salinity of 24 °/oo, temperature of 18° C., and pH of 7.9.

Animals and sediment from the drop zone area were collected before and after the release of the labeled sediment. Samples of sediment and sea water, and of blue crabs; Atlantic croaker; star drum, *Stellifer lanceolatus:* flounder, *Paralichthys* sp.; and American menhaden, *Brevoortia tyrannus,* were collected 1 week prior to the first drop in order to measure background activity. Organisms and sediment were collected again on the third day following the release of the labeled sediment. In addition to those species collected before the release of labeled sediment, the white

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shrimp, *Penaeus setiferus*, appeared in samples taken after the release. Sediment samples from the drop zone were composed mostly of sand. Additional information on the sediments is given by the U.S. Army Corps of Engineers (1964).

Cages containing various estuarine organisms were placed at six stations around the proposed drop zone 24 hours before the scheduled release (fig. 4). Test animals at each station included 25 blue crabs; 50 oysters, *Crassostrea virginica;* and 50 mummichogs, *Fundulus heteroclitus*. Ten croakers were included at stations IV, V, and VI. The blue crabs were kept in separate cages to prevent predation on the other test animals. Also, at each station, plastic petri dishes filled with montmorillonite clay were placed in minnow traps to test for adsorption of gold 198. Five to ten animals of each species were removed from the cages for each sample.

The radioactivity content of the field samples was measured at the Bureau of Commercial Fisheries Radiobiological Laboratory, Beaufort, N.C., 110 miles from the sampling area. The detector system consisted of a 3-inch NaI(Tl) crystal coupled to a single-channel gamma spectrometer. Sediment and biological samples were placed in individual plastic bags, packed in an ice chest, and transported to the laboratory as soon as possible after sampling. Water samples were held in screw cap jars. If the water samples were found to be radioactive, the water was Millipore-filtered and counted again, along with the separated material, to determine whether the radioactive gold was associated with suspended material.

The various samples were measured for radioactivity in a manner that permitted the comparison of organisms, sediments, and water. To make these comparisons, it was necessary that the radioactivity in all of the samples be measured under similar conditions of geometry. Organisms containing gold 198 were measured for radioactivity before and after being dissolved in nitric acid and diluted to 900 ml. A factor was thus obtained for converting measurements made on the intact organisms to measurements which would be obtained after dissolving and diluting the organisms to 900 ml. A factor was obtained for the sediments in a similar manner, except that no acid was used and Calgon was added as a wetting agent. No preparation was necessary to measure gold 199 in the 900 ml. samples of water. Since radioactivity measurements in intact organisms and sediments could be converted to measurements based on their being contained in a 900-ml. volume of water, and since all measurements of water were for 900 ml., it was possible to compare activity contained in these three types of samples.

The radioactivity content of water, sediments, and biota varied widely between stations. Biological samples from stations III and VI did not contain measurable amounts of radioactivity at any time (table 5). As one would expect, biological samples from station II, located directly in the drop zone, contained higher concentrations of radioactivity than those of other stations. Lateral dispersion of radiogold was indicated by the increase in activity in the crabs and oysters from stations I and IV after 41 hours elapsed time.

The second application of gold appeared to have little or no effect on the levels of concentration in the samples, except perhaps those in station IV. Oysters and crabs accumulated radioactivity to maximum level 17 hours after the first radiogold

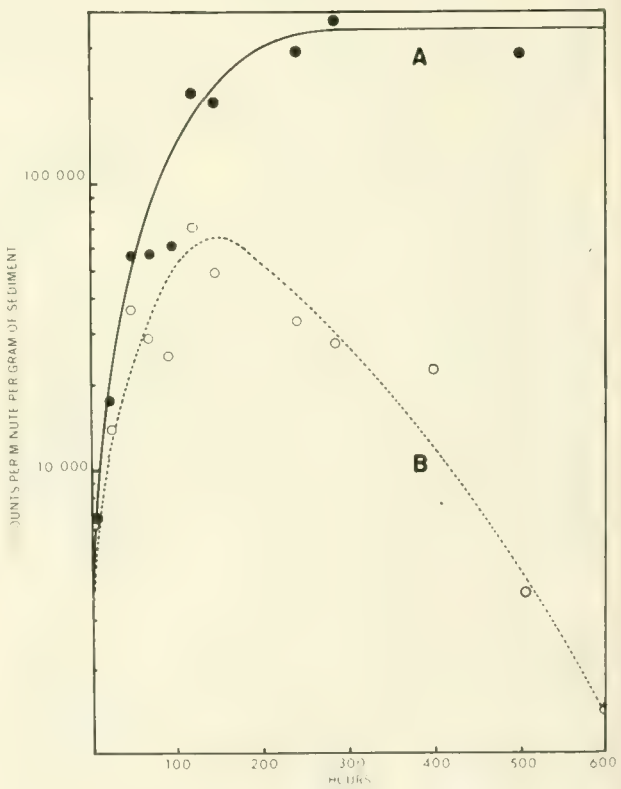

FIGURE 5.—Radioactivity content of biota and sediments from Cape Fear River after release of gold tracer.

application (fig. 5). However, this occurred 5 hours before the second application.

Background samples of biota and water collected in the drop zone area 1 week prior to the release of the labeled sediments did not contain measurable gamma activity in the energy range between 100 and 400 kiloelectron volts (Kev), the setting which includes the photopeak of radioactive gold. However, sediment samples contained gamma activity ranging from 367 to 729 counts per minute per kg. wet weight at this setting. Biota, water, and sediments collected from the same area 41 hours after the release did not show an increase in radioactive content over the background samples.

TABLE 5.—*Radioactive gold content of field samples* [1]

[Activity m.μc/kg.]

Elapsed time in hours	Sample	Station					
		I	II	III	IV	V	VI
1	Water	—	6.8	—	—	—	—
	Sediment	—	NS	—	—	—	—
	Fish	—	NS	—	—	—	—
	Oyster	—	23.8	—	—	—	—
	Clay	—	45.6	—	—	—	—
	Crab	—	27.3	—	—	—	—
17	Water	5.1	4.7	2.96	4.2	4.12	NS
	Sediment	NS	60.3	NS	—	NS	—
	Fish	NS	NS	NS	—	36.90	—
	Oyster	NS	70.9	NS	—	40.22	—
	Clay	NS	—	—	—	—	—
	Crab	NS	61.6	NS	—	—	—
41	Water	NS	NS	NS	NS	NS	NS
	Sediment	NS	NS	NS	NS	NS	NS
	Fish	NS	NS	NS	NS	NS	NS
	Oyster	15.7	31.1	NS	24.5	14.1	NS
	Clay	—	NS	—	—	—	—
	Crab	14.8	22.9	NS	24.9	19.0	—
144	Water	—	—	—	NS	—	NS
	Sediment	—	—	—	NS	—	NS
	Fish	—	—	—	NS	—	NS
	Oyster	—	—	—	NS	—	NS
	Crab	—	—	—	NS	—	NS

[1] NS indicates activity not significantly greater than background; dash indicates no sample was taken.

DISCUSSION

The potential hazards accompanying the release of radioactive material into the marine environment should be investigated so that the most dangerous situation possible is evaluated. The accumulation of radioactive gold from sea water by the animal community contained in the large tank was a simulation of this extreme situation: The closed system offered no opportunity for the animals to escape the contaminated area, and there was neither inflow of nonactive sea water nor outflow of contaminated water. Under these controlled conditions, organisms and sediments accumulated the isotope from sea water, with crabs and filter-feeding organisms accumulating the isotope to the greatest extent.

Surface sorption of radioactive gold, no doubt, is an important factor contributing to rapid accumulation by marine organisms and sediments. This is based on the observation that 50 percent of the isotope added to the water in an experimental environment moved very quickly to organisms and sediments within the tank. It is known that biological accumulation of a radiosotope by sorption occurs rapidly. Further, it has been shown that gold occurs in sea water in a particulate state. Since particles have difficulty passing through biological membranes, surface sorption is most important in their accumulation by marine organisms. The importance of surface sorption in the accumulation of radioactive gold by organisms was demonstrated experimentally when the radioactive content of clams buried in sediment was shown to be less than that of clams resting on the smooth bottom surface of the tank. Although the buried clams had less area exposed, the same average amount of water should have passed through their siphons as through the siphons of those resting on the bottom. If all the accumulation of gold had been a result of metabolism, the gold content of buried and exposed organisms should have been the same.

The literature contains several references pertaining to the surface accumulation of material from sea water. As early as 1937, Harvey demonstrated that particulate matter such as ferric hydroxide was associated with phytoplankton cells by electrostatic attraction to external surfaces. Also, Goldberg (1952) observed that particulate and colloidal iron was utilized by *Asterionella japonica*. Rice and Willis (1959) showed that particulate cerium 144 became attached to *Nitzschia* cells as a result of particles and cells coming in contact with each other and sticking.

The distribution of this isotope within the animals was observed by placing large quantities of radioactive gold directly into the gut of several estuarine animals. Those organs associated with excretion retained more gold 199 than did others, suggesting that the gold was simply being excreted rather than being stored or utilized. The principal route of gold administered as an oral dose to mammals was reported by Spector (1956) to be directly from the alimentary tract to the feces with

little absorption along the way. In the present study, little, if any, radioactive gold was found in the organs of fish that were fed this isotope sorbed onto clay.

In field studies, animals and sediment maintained in cages in the drop zone sorbed little activity. This could have been caused by the tremendous dilution by river water and strong currents, and to the short physical half-life of the gold isotope. Since it was demonstrated experimentally that the animals retained little activity from ingested labeled sediment particles, the initial accumulation of activity was perhaps from unbound gold that was not sorbed onto sediments in the mixing hopper but remained in the water phase of the slurry.

Since gold is not biologically essential and is not concentrated significantly by estuarine animals, the isotope gold 198, with its short physical half-life of 2.7 days, appeared to be a safe and effective tracer for following sediment movement. Even though as much as 5 c. of gold 198 were released in the Cape Fear River at one time, the maximum concentration found in any of the animals tested was 70.9×10^{-5} μc. per g. of oyster at station II (table 5). This is slightly in excess of the maximum permissible concentration (MPC) for gold 198 in water effluent released in an unrestricted area, i.e., 5×10^{-5} μc./ml. (Code of Federal Regulations, 1960). However, station II was purposely located in the drop zone so that the caged animals would be subjected to the most extreme conditions of contamination. There is no evidence now that radiation from the low levels of gold 198 involved in these investigations affected the biota.

ACKNOWLEDGMENTS

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A GENERIC KEY TO THE PROTOZOEAN, MYSIS, AND POSTLARVAL STAGES OF THE LITTORAL PENAEIDAE OF THE NORTHWESTERN GULF OF MEXICO [1]

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ABSTRACT

An illustrated key presenting criteria for differentiating the stages and substages of Gulf of Mexico penaeid larvae (and post larvae) from comparable stages of the more common nonpenaeids is presented. A second key permits generic identification of penaeid protozoean, mysis, and postlarval stages. All genera are illustrated, and a table of important diagnostic characters is included.

Shrimp of the Family Penaeidae which support valuable commercial fisheries in the northwestern Gulf of Mexico are being studied comprehensively by fishery scientists at the Bureau of Commerical Fisheries Biological Laboratory in Galveston, Tex. To properly manage such fisheries, it is necessary to fully understand the dynamics of the shrimp populations upon which they depend. This capability requires, in turn, as complete a knowledge as possible of the life history of the species involved.

Studies of the early (planktonic) life history of the Gulf's commercially important shrimps have been hampered by difficulties encountered in distinguishing larvae of these species from those of lesser importance. Fortunately, there has been considerable research on the description and general systematics of larval and postlarval Penaeidae both in this country and abroad. As a result, all the littoral genera known to occur in the northwestern Gulf of Mexico have had representatives—although not necessarily of indigenous species—at least partially described. The principal problem, therefore, was one of consolidating all the available information and ascertaining what portions of it might help describe the local penaeid larvae. The intent of this paper is to present criteria that will aid in distinguishing larvae and postlarvae of the genus *Penaeus* Fabricius from those of *Parapenaeus* Smith, *Sicyonia* H. Milne Edwards, *Solenocera* Lucas, *Trachypeneus* Alcock, and *Xiphopeneus* Smith, the five other littoral genera found locally.

The material made available for examination during this study was collected systematically between March 1959 and March 1960 and during January to December 1961. From January to September 1961, plankton was sampled with a Gulf-V net to depths of 45 fathoms between Cameron, La., and Freeport, Tex. In September, the sampling program was enlarged to include the area between Morgan City, La., and the mouth of the Colorado River, Tex.

Although various larval stages of several species represented in this area had been recorded, there were no established criteria for differentiating the penaeid larvae. Consequently, as new or theretofore unrecognized penaeid larvae and postlarvae were found in the plankton samples, they were assigned a code number and a reference sketch of them was made. Through the use of descriptions

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taken from the literature, and by comparison with larvae reared in the laboratory from eggs of known parentage, planktonic larvae were assigned to genera. Subsequent examination of accumulated material revealed the presence of protozoeal, mysis, and postlarval characters which remained constant within each genus. These characters were, in turn, used as criteria to construct a key to local genera. A key based for the most part on planktonic rather than laboratory-reared material has its limitations, but the scarcity of information concerning penaeid larvae from this area nevertheless justifies its presentation at this time.

Despite the fact that *Penaeus aztecus* Ives (brown shrimp); *P. duorarum* Burkenroad (pink shrimp); *Sicyonia brevirostris* (Stimpson) and *S. dorsalis* (Kingsley) (rock shrimps); *Trachypeneus similis* (Smith); and *Xiphopeneus krøyeri* (Heller) (seabob) have been reared successfully through the nauplial stage under laboratory conditions, the nauplii were found to be so similar as to defy attempts to fit them into a key. Although differences in setation are minor or absent, the lack of a dorsal protuberance (fig. 1f), as well as larger relative size, serves to distinguish nauplii of the genus *Penaeus*. In genera other than *Penaeus*, this protuberance is present on the dorsal surface of the body above the insertion of the second antennae.

Within a given developmental stage (e.g., Nauplius II, Protozoea I, etc.), the size ranges of penaeid larvae as a whole are extremely variable, although in the northern Gulf, larvae of the genus *Penaeus* are generally larger than those belonging to comparable stages of other genera. Hudinaga (1942) found that the protozoeal stages of *P. japonicus* Bate exhibited intermolt growth, the occurrence of which may also be true for other stages as suggested for nauplii of *Xiphopeneus krøyeri* by Renfro and Cook (1963). The possibility also exists that larvae (and postlarvae) of the same species grow dissimilarly at different times of the year. Since the relative size at each stage overlaps considerably between, as well as within, the various genera, it should be used with discretion for purposes of identification.

While the number of substages in each penaeid larval stage described in the literature has been found to vary, the normal situation in the northwestern Gulf of Mexico—as ascertained from material in plankton collections—seems to be five nauplial, three protozoeal, and three mysis substages. Examples of departure from this sequence are provided by the larvae of *Sicyonia brevirostris* which, when reared in the laboratory, appeared to pass through four mysis substages, and by those of *Parapenaeus* sp. which, as determined from sample material, also have at least four. Such apparent anomalies suggest that descriptions of penaeid larvae obtained either from rearing experiments or plankton samples must be viewed with caution until more is known of the effects of environmental factors on early growth and morphology.

Table 1, in addition to presenting the principal diagnostic characters included in the following key, also furnishes other valuable characters for distinguishing larvae and postlarvae.

All illustrations are intended to clarify generic characteristics and do not represent particular species.

KEY TO STAGES AND SUBSTAGES OF PENAEID LARVAE AND EARLY POSTLARVAE

1	Body simple, unsegmented; three pairs of appendages arising from anterior portion of body, first unbranched, second and third branched; paired caudal spines arise from posterior end of body (Nauplius)---- 2
	Not as above---- 7
2(1)	Body pear shaped; pairs of caudal spines of equal length, extending straight posteriorly; lateral setae on appendages arise singly or in pairs; appendages lack spines or processes such as would be utilized for feeding purposes; carapace present only as a close-fitting rudiment in later stages (Penaeid nauplius fig. 1)---- 3
	One or more of the following characters present: body elliptical; pairs of caudal spines of unequal length or extending medianly, crossing one another; lateral setae on appendages arising in clusters; spines or processes such as would be utilized for feeding purposes present; a well-developed or prominent carapace present Nonpenaeid nauplius
3(2)	Five setae on exopod of second antenna; one pair of caudal spines; surface of body between insertion of caudal spines convex-- Nauplius I (fig. 1a)
	More than five setae on exopod of second antenna; one or more pairs of caudal spines; surface of body between insertion of caudal spines not convex---- 4
4(3)	Six setae on exopod of second antenna; usually one, sometimes two, pairs of caudal spines; surface of body between insertion of caudal spines flat---- Nauplius II (fig. 1b)

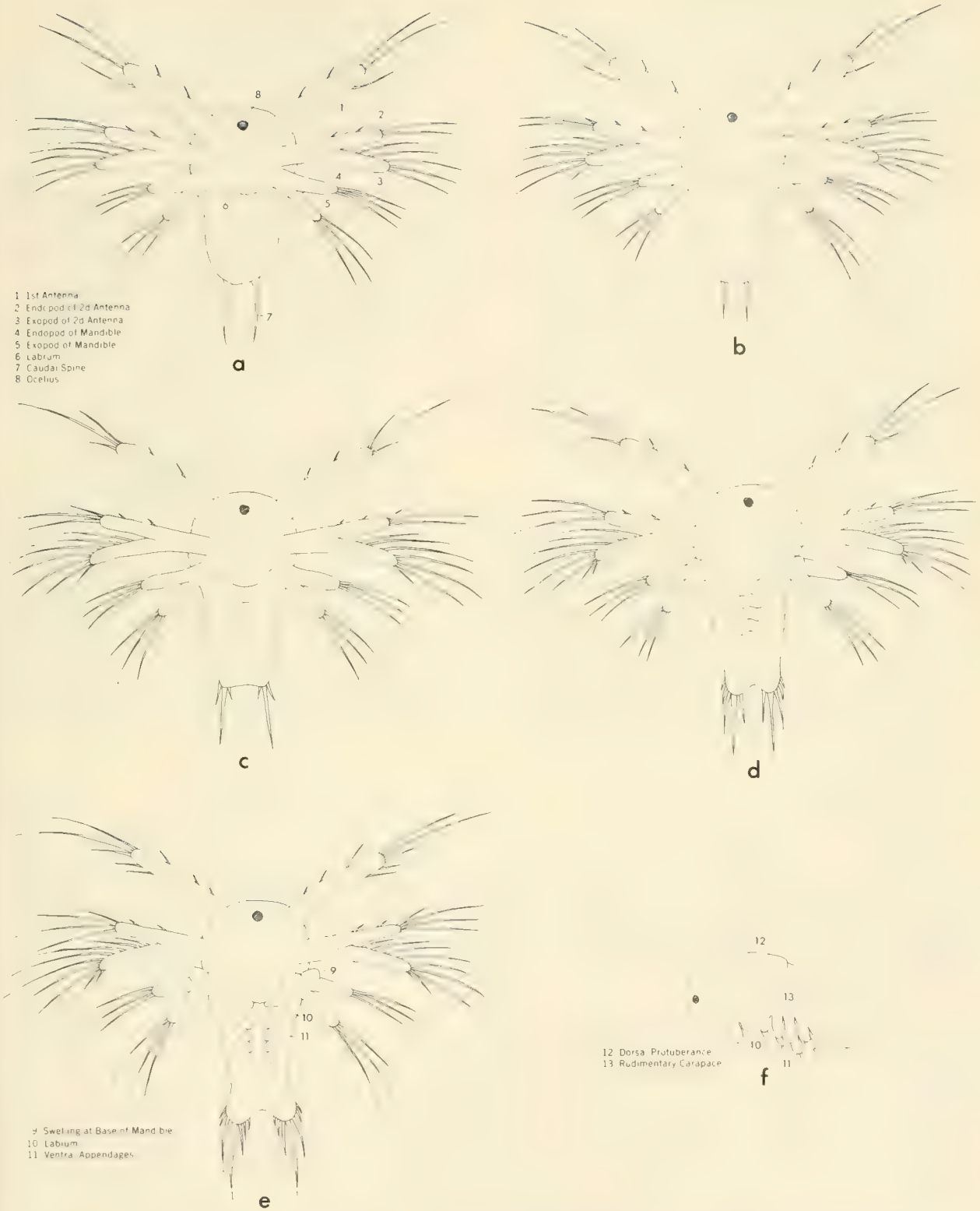

FIGURE 1.—Penaeid nauplii: *a*, Nauplius I; *b*, Nauplius II; *c*, Nauplius III; *d*, Nauplius IV; *e*, and *f*, Nauplius V.

More than six setae on exopod of second antenna; usually three or more pairs of caudal spines; surface of body between insertion of caudal spines concave 5

5(4) Seven setae on exopod of second appenadge; usually three, sometimes four, pairs of caudal spines; surface of body between insertion of caudal spines slightly concave; no swelling at base of mandible ..... Nauplius III (fig. 1c)

More than seven setae on exopod of second antenna; usually more than four pairs of caudal spines; surface of body between insertion of caudal spines deeply concave; base of mandible swollen 6

6(5) Eight setae on exopod of second antenna; usually five, sometimes six, pairs of caudal spines; slight swelling at base of mandible; endopod of mandible never transparent; rudimentary ventral appendages posterior to third appendages

Nauplius IV (fig. 1d)

Nine setae on exopod of second antenna; usually seven, sometimes six, pairs of caudal spines; large subconical protuberance at base of mandible; endopod of mandible frequently transparent; ventral appendages prominent

Nauplius V (fig. 1e)

7(1) Large, prominent, carapace followed by a slender segmented thorax and an abdomen which may or may not be segmented; two pairs of prominent appendages arising from anterior portion of body, the first unbranched, the second branched; prominent labrum present (Protozoea) 8

Not as above 11

8(7) Carapace does not completely cover thorax; abdomen bifurcate posteriorly, with each furca bearing at least seven spines; biramous first and second maxillipeds well developed, the third absent or present only as a rudiment; usually, no spines arise from posterior half of carapace; if spines present, a dorsal organ (fig. 2d) is present (Penaeid protozoea fig. 2) 9

One or more of the following characters present: carapace completely covers thorax; abdomen not bifurcate; caudal furcae bear less than seven pairs of spines; first and second maxillipeds not well developed or third maxilliped well developed; if numerous spines arise from posterior portion of carapace, dorsal organ not present

Nonpenaeid protozoea

9(8) Eyes sessile, beneath carapace; pereiopods absent; abdomen unsegmented

Protozoea I (fig. 2a)

Eyes stalked; pereiopods present at least as small buds; abdomen segmented 10

10(9) Uropods not present externally, may be seen beneath cuticle; pereiopods present only as small buds; first five abdominal segments without dorsal spines ..... Protozoea II (fig. 2b)

Uropods present externally; pereiopods rudimentary, but biramous and prominent; first five abdominal segments with dorsal spines

Protozoea III (fig. 2c)

11(7) Carapace closely fitting with a rostrum that extends anteriorly between the eyes; five pairs of biramous pereiopods present, with the exopods elongate and bearing numerous setae which make them appear brushlike; six-segmented abdomen followed by telson and biramous uropods; pleopods, if present, rudimentary and nonfunctional (Mysis) 12

Carapace closely fitting with a rostrum extending anteriorly between the eyes; five pairs of pereio-

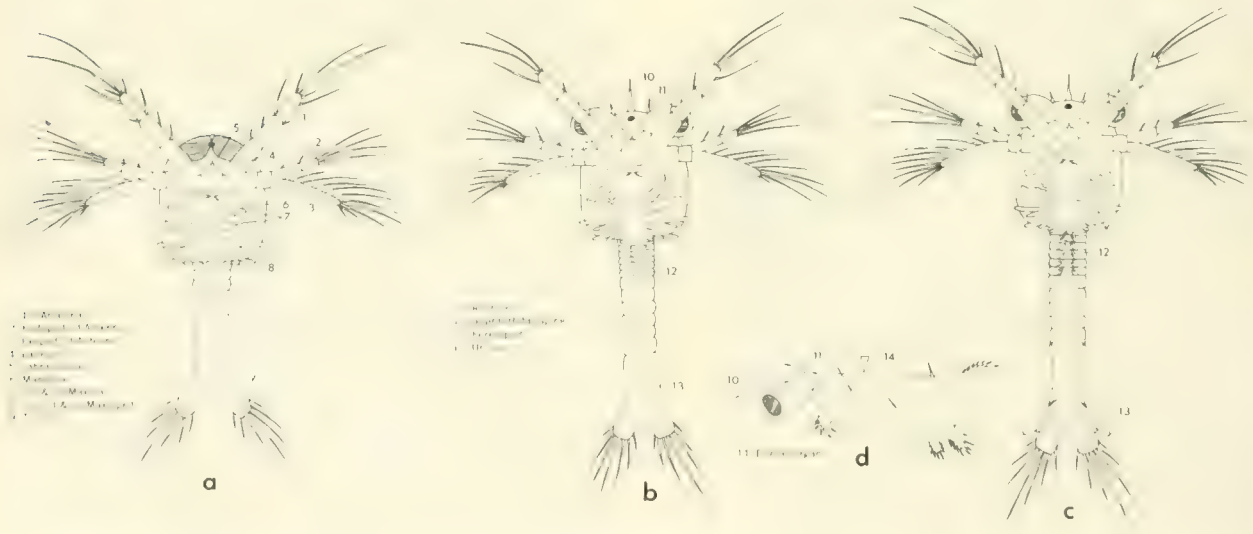

FIGURE 2.—Penaeid protozoeae: *a*, Protozoea I; *b*, Protozoea II; *c*, Protozoea III; *d*, Protozoea III, carapace.

pods present, with exopods absent or present only as rudiments; six-segmented abdomen followed by telson and biramous uropods; five pairs of setose, functional pleopods present (Postlarvae)---------- 15

12(11) First three pairs of pereiopods cleft to form rudimentary chelae; pleura of first abdominal segment overlap second; antennal blades present; pleopods develop on first five abdominal segments simultaneously although they are not necessarily of equal length; telson narrow and notched medianly; uropods without statocysts; usually, no spines originate from posterior half of carapace and margins of carapace not serrate; if spines or serrations present, a dorsal organ also present (Penaeid mysis fig. 3)---------- 13

One or more of following characters present: first three pereiopods not cleft to form rudimentary chelae; pleura of second abdominal segment overlap first; antennal blades absent; pleopods may not be present on all abdominal segments; telson broad and fan shaped or not notched medianly; uropods with statocyst; spines originate from posterior half of carapace or margins of carapace serrate, with no dorsal organ present---------- Nonpenaeid mysis

13(12) Pleopods absent---------- Mysis I (fig. 3a)

Pleopods present---------- 14

14(13) Pleopods small and unjointed-- Mysis II (fig. 3b)

Pleopods long and jointed--- Mysis III (fig. 3c)

15(11) First three pairs of pereiopods chelate; pleura of first abdominal segment overlapping second; five pairs of functional pleopods present; gills covered by carapace; antennal blades present

Penaeid postlarva (fig. 4)

One or more of the following characters present: first three pairs of pereiopods not chelate; pleura of second abdominal segment overlapping first; less than five pairs of functional pleopods present; gills extending from beneath carapace; antennal blades absent---------- Nonpenaeid postlarva

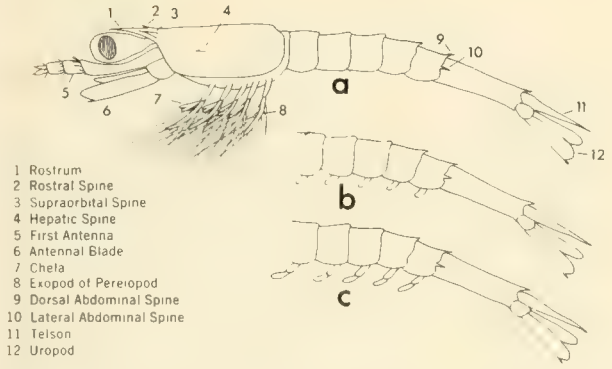

FIGURE 3.—Penaeid myses: *a*, Mysis I; *b*, Mysis II; *c*, Mysis III.

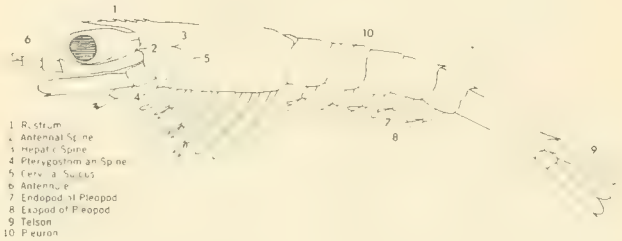

FIGURE 4.—Penaeid postlarva.

KEY TO GENERA OF PENAEID LARVAE AND POSTLARVAE

PROTOZOEAE

(Fig. 5)

1 Number of lateral setae on endopod of second appendage 1+1+2 [2]---------- *Penaeus*
Number of lateral setae on endopod of second appendage not 1+1+2---------- 2

2(1) First appendage about twice as long as second; no spine on anterior margin of labrum; number of lateral setae on endopod of second appendage 1+2+3---------- *Sicyonia*
First and second appendages of nearly equal length; a spine present on anterior margin of labrum; number of lateral setae on endopod of second appendage may be 1+2+3---------- 3

3(2) Number of lateral setae on endopod of second appendage 1+2+2, 1+2+3, or 2+2+2- *Parapenaeus*
Number of lateral setae on endopod of second appendage not 1+2+2 or 2+2+2---------- 4

4(3) Number of lateral setae on endopod of second appendage 2+2+3---------- *Solenocera*
Number of lateral setae on endopod of second appendage 2+2---------- 5

5(4) Four long, terminal setae on endopod of second appendage---------- *Trachypeneus*
Four long and one short terminal setae on endopod of second appendage---------- *Xiphopeneus*

[2] Starting with proximal seta, the number of lateral setae at each point of insertion is recorded.

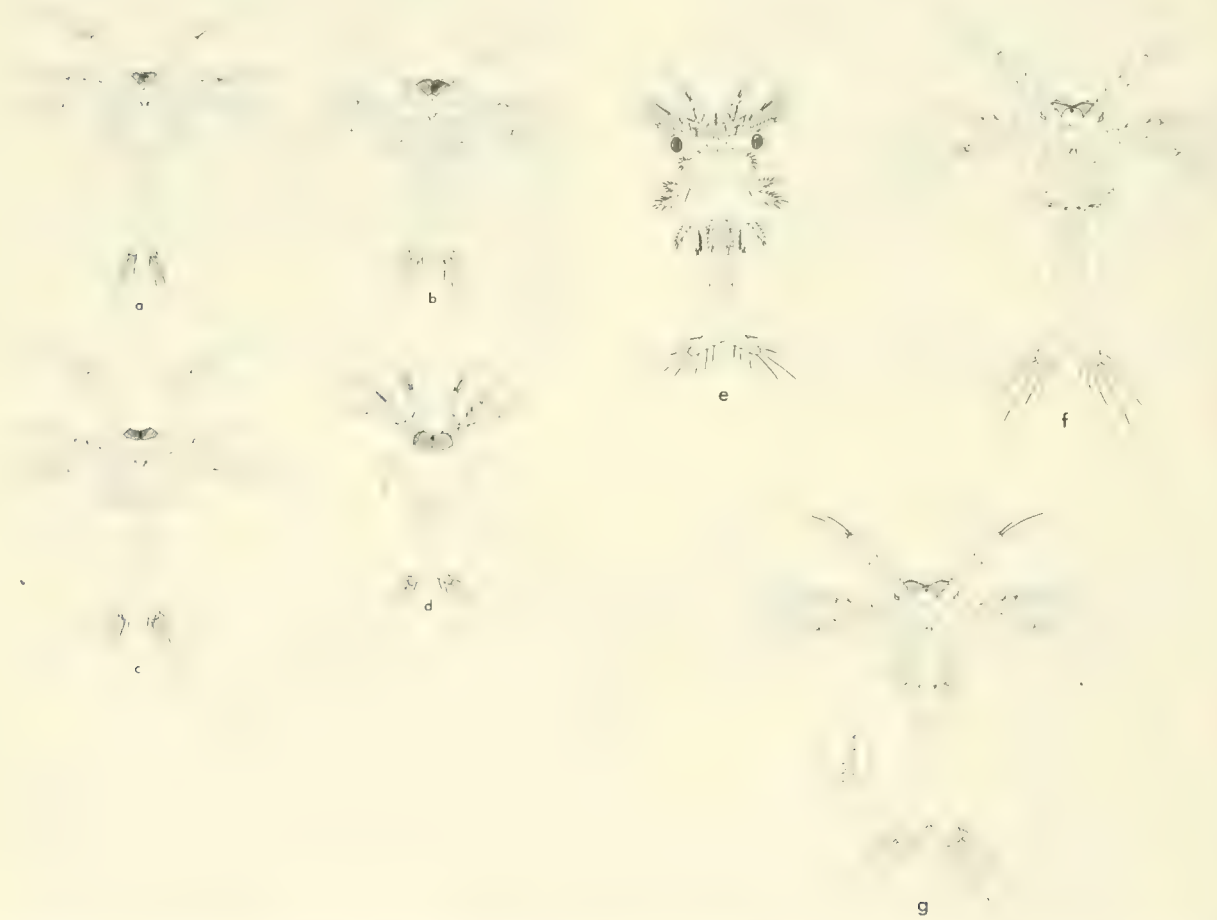

FIGURE 5. Penaeid protozoeae: *a*, *Parapenaeus*, Protozoea I; *b*, *Penaeus*, Protozoea I; *c*, *Sicyonia*, Protozoea I; *d*, *Solenocera*, Protozoea I; *e*, *Solenocera*, Protozoea II; *f*, *Trachypeneus*, Protozoea I; *g*, *Xiphopeneus*, Protozoea I.

MYSES

(Fig. 6)

1 Carapace and abdomen with many spines; dorsal organ present on dorsal surface of carapace *Solenocera*

Carapace and abdomen without many spines; dorsal organ absent 2

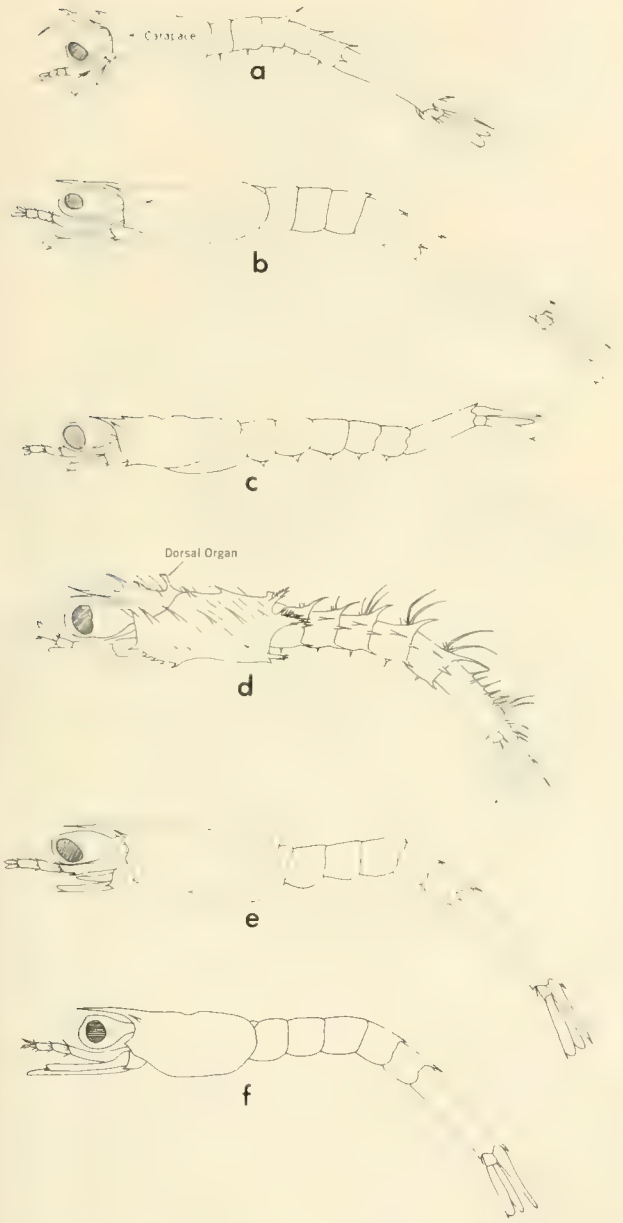

FIGURE 6.—Penaeid myses: *a*, *Parapenaeus*, Mysis I; *b*, *Penaeus*, Mysis I; *c*, *Sicyonia*, Mysis I; *d*, *Solenocera*, Mysis I; *e*, *Trachypeneus*, Mysis I; *f*, *Xiphopeneus*, Mysis I.

2(1) Dorsomedian spines not present on first five abdominal segments ..... *Sicyonia*
Dorsomedian spine present on at least fourth and fifth abdominal segments 3

3(2) Dorsomedian spine not present on third abdominal segment 4
Dorsomedian spine present on third abdominal segment 5

4(3) Lateral spine present on fifth abdominal segment; rostrum shorter than eye ..... *Trachypeneus*
Lateral spine not present on fifth abdominal segment; rostrum as long as or shorter than eye *Xiphopeneus*

5(3) Dorsomedian spine on third abdominal segment elongate ..... *Parapenaeus*
Dorsomedian spine on third abdominal segment not elongate ..... *Penaeus*

POSTLARVAE

(Fig. 7)

1 Total length 6.0 mm. or less [3] 3
Total length greater than 6.0 mm 2

2(1) Total length 6.0 mm. to 12.0 mm 5
Total length 12.0 mm. to 25.0 mm 10

3(1) No terminal spines on telson ..... *Sicyonia*
Terminal spines present on telson 4

4(3) Medioterminal spines of telson longer than those adjacent to it ..... *Trachypeneus*
Medioterminal spine of telson equal in length to those adjacent to it ..... *Penaeus*

5(2) First abdominal segment with dorsal anteromedian spine ..... *Sicyonia*
First abdominal segment without dorsal anteromedian spine 6

6(5) Pterygostomian spine present; pleopods of fifth abdominal segment with exopods and endopods of equal length 7
Pterygostomian spine absent; pleopods of fifth abdominal segment with endopods inferior to exopods 8

7(6) Antennules round; no cervical sulcus on carapace; rostrum curved ..... *Parapenaeus*
Antennules flattened; well-defined cervical sulcus present on carapace; rostrum straight ..... *Solenocera*

8(5) Antennal spine absent or minute; if present, subrostral teeth also present ..... *Penaeus*
Antennal spine very prominent; no subrostral teeth 9

9(8) Rostrum shorter than eye ..... *Trachypeneus*
Rostrum longer than eye ..... *Xiphopeneus*

10(2) Rostrum usually with ventral teeth and shallowly compressed ..... *Penaeus*
Rostrum without ventral teeth and broadly compressed 11

11(10) Pterygostomian spine present 12
Pterygostomian spine absent 13

[3] Early *Xiphopeneus* postlarvae probably fall in the <6.0-mm. category, but none in this size range was noted during the study.

12(11) Antennules flattened; cervical sulcus present; sixth abdominal segment short and slightly curved ..... *Solenocera*
Antennules round; cervical sulcus absent; sixth abdominal segment long and straight ..... *Parapenaeus*

13(11) Rostrum longer than eye ..... *Xiphopeneus*
Rostrum shorter than eye 14

14(13) First abdominal segment with anteromedian spine on dorsal surface; sixth abdominal segment short ..... *Sicyonia*
First abdominal segment without anteromedian spine on dorsal surface; sixth abdominal segment elongate ..... *Trachypeneus*

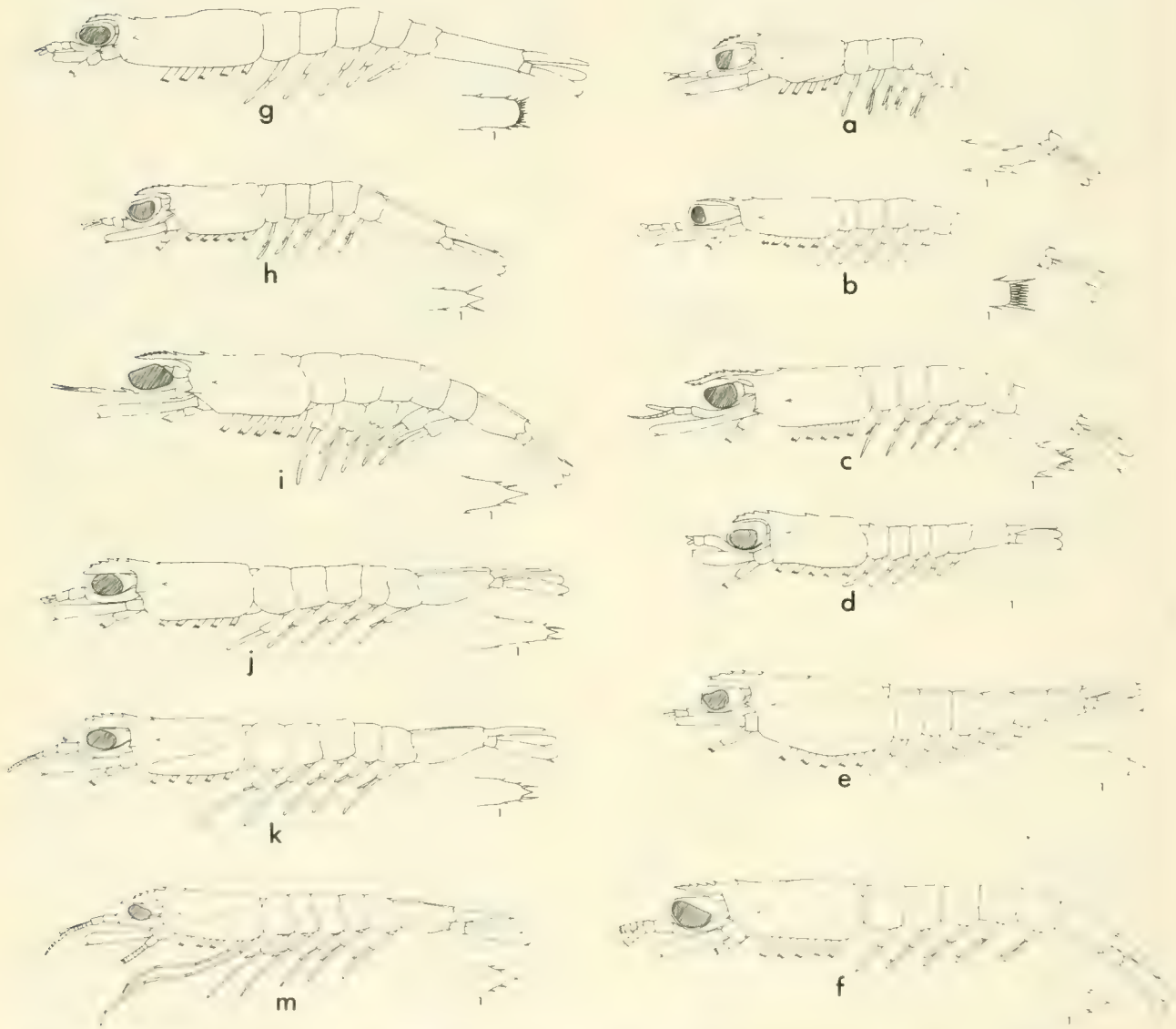

FIGURE 7.—Penaeid postlarvae: *a*, *Parapenaeus* postlarva, 8.0 mm.; *b*, *Penaeus* postlarva, 6.0 mm.; *c*, *Penaeus* postlarva, 15.0 mm.; *d*, *Sicyonia* postlarva, 5.0 mm.; *e*, *Sicyonia* postlarva, 14.0 mm.; *f*, *Solenocera* postlarva, 7.0 mm.; *g*, *Trachypeneus* postlarva, 6.0 mm.; *h*, *Trachypeneus* postlarva, 10.0 mm.; *i*, *Trachypeneus* postlarva, 25.0 mm.; *j*, *Xiphopeneus* postlarva, 6.0 mm.; *k*, *Xiphopeneus* postlarva, 7.5 mm.; *m*, *Xiphopeneus* postlarva, 12.0 mm.; *l*, Tip of telson.

TABLE 1.—*Characters of diagnostic importance in distinguishing genera during the early life history stages of the littoral Penaeidae occurring along the northern Gulf coast*

Stage and structure	*Parapenaeus*	*Penaeus*	*Sicyonia*	*Solenocera*	*Trachypeneus*	*Xiphopeneus*
PROTOZOEAE–GENERAL						
Relative lengths of 1st and 2d appendages.	Approximately equal.	Approximately equal.	First about twice as long as second.	Approximately equal.	First about 1½ as long as second.	First about 1½ as long as second.
Spine on labrum	Small	Small	Absent	Very long	Small	Small.
Telson	Narrow and deeply notched.	Medium width and notch.	Medium width and notch	Wide and shallowly notched.	Medium width and notch.	Medium width and notch.
Dorsal surface of carapace	Smooth	Smooth	Small hump	Spines and dorsal organ.	Small hump	Small hump.
Setation of endopod of second appendage.	Variable	1+1+2 lateral	1+2+3 lateral	2+2+3 lateral	2+2 lateral, 4 terminal.	2+2 lateral, 5 terminal.
PROTOZOEAE I						
Projection on front of carapace.	Pointed	Round	Round	Pointed	Round	Round.
Third maxilliped	Small, biramous, no setae.	Absent or present as small uniramous bud.	Small, biramous, no setae.	Small, biramous, with setae.	Small, biramous, with setae.	Small, biramous, with setae.
Spines on carapace	None	None	None	Four pairs	None	None.
PROTOZOEAE II						
Rostrum	Long	Long	Short	Long	Long	Long.
Supraorbital spines	Two pairs	One pair	Absent	One pair with many branches.	Absent	Absent.
PROTOZOEAE III						
Rostrum	Long	Long	Short	Long	Long	Long.
Supraorbital spines	One pair	One pair	Absent	One pair	Absent	Absent.
Dorsomedian spines of abdomen.	Present on six segments.	Present on first five segments.	Present on first five segments.	Present on first five segments.	Present on first five segments.	Present on first five segments.
Posterolateral spines of abdomen.	Present on fourth, fifth, and sixth segments.	Present on fifth and sixth segments.	Present on fifth segment.	Present on sixth segment	Present on fifth and sixth segments.	Present on fifth and sixth segments.
Ventrolateral spine on sixth segment.	One pair	One pair	One pair	One pair	Two pairs	Two pairs.
MYSIS						
Rostrum	Elongate, toothed, broadened at base.	Elongate, smooth, not broadened at base.	Short, toothed, not broadened at base.	Elongate, toothed, not broadened at base.	Elongate, toothed, not broadened at base.	Elongate, toothed, not broadened at base.
Superaorbital spine	Present	Present	Present	Present	Present	Present.
Hepatic spine	Present	Present	Absent	Present	Absent	Absent.
Ventromedian spines of abdomen.	Present	Absent	Present	Present	Absent	Absent.
Posterolateral spines of abdomen.	Present on fifth and sixth segments.	Present on fifth and sixth segments.	Absent	Present on first five segments.	Present on fifth segment.	Absent.

TABLE 1.—*Characters of diagnostic importance in distinguishing genera during the early life history stages of the littoral Penaeidae occurring along the northern Gulf coast*—Continued

Stage and structure	*Parapenaeus*	*Penaeus*	*Sicyonia*	*Solenocera*	*Trachypeneus*	*Xiphopeneus*
PROTOZOEAE—Continued						
MYSIS—Continued						
Dorsomedian spines of abdomen.	Present on third, fourth, fifth, and sixth segments. Spine of third segment elongate.	Present on third, fourth, fifth, and sixth segments.	Present on sixth segment only.	Present on six segments.	Present on fourth, fifth, and sixth segments.	Present on fourth, fifth, and sixth segments.
POSTLARVAE						
FIRST TO 6.0-MM. POSTLARVAE:						
Rostrum	[First postlarva begins at about 8.0 mm.]	Straight	Curved	[First postlarva begins at about 7.0 mm.]	Curved	None examined.
Anteromedian spine on first abdominal segment.		Absent	Present		Present	
Sixth abdominal segment		Elongate	Short		Elongate	
6.0- TO 12.0-MM. POSTLARVAE:						
Anteromedian spine of first abdominal segment.	Absent	Absent	Present	Absent	Absent	Absent.
Length of pleopods	All equal	All equal	Fifth pleopod shorter than first.	Fifth pleopod shorter than first.	All equal	All equal.
Relative lengths of endopod and exopod of fifth pelopod.	Approximately equal.	Endopod absent or inferior.	Endopod absent	Approximately equal.	Endopod inferior	Endopod inferior, exopod elongate.
Pterygostomian spine	Present	Absent	Absent	Present	Absent	Absent.
Antennal spine	Present	Absent	Present	Present	Present	Present.
Antennules	Round	Round	Round	Flattened	Round	Round.
Sulcae of carapace	Absent	Absent	Absent	Cervical sulcus	Absent	Branchio-cardiac sulcus.
Rostrum	Curved, elongate	Straight, elongate	Straight, short	Straight, short	Curved, short	Curved, elongate.
Sixth abdominal segment	Elongate, straight	Elongate, straight	Short, straight	Medium, curved ventrally.	Medium, straight	Medium, straight.
12.0- TO 25.0-MM. POSTLARVAE:						
Rostrum	Curved, elongate, subrostral teeth absent.	Curved, elongate, subrostral teeth present.	Straight, short, subrostral teeth absent.	Straight, medium, subrostral teeth absent.	Curved, medium, subrostral teeth absent.	Curved, elongate, subrostral teeth absent.
Pterygostomian spine	Present	Absent	Absent	Present	Absent	Absent.
Antennules	Round	Round	Round	Flattened	Round	Round.
Sulcae of carapace	Absent	Absent	Absent	Cervical sulcus	Absent	Branchio-cardiac sulcus.
Sixth abdominal segment	Elongate, straight	Elongate, straight	Short, straight	Medium, curved ventrally.	Medium, straight	Medium, straight.
Anteromedian spine on first abdominal segment.	Absent	Absent	Present	Absent	Absent	Absent.

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Ray S. Wheeler and Robert F. Temple offered many helpful suggestions during the course of this study, and Daniel Patlan assisted with the drawings.

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MIGRATIONS AND GEOGRAPHIC DISTRIBUTION OF PINK SHRIMP, *PENAEUS DUORARUM*, OF THE TORTUGAS AND SANIBEL GROUNDS, FLORIDA [1]

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BUREAU of COMMERCIAL FISHERIES BIOLOGICAL FIELD STATION, MIAMI, FLA.

ABSTRACT

Pink shrimp, *Penaeus duorarum*, frequent the estuarine waters of south Florida as juveniles. As adults, they support valuable fisheries on the offshore Tortugas and Sanibel trawling grounds in the Gulf of Mexico. To study the Tortugas and Sanibel shrimp stocks as biological units, 15 mark-recovery experiments in which biological stains were the marking agents were made. These experiments (1) indicated timing and direction of shrimp migrations; (2) delineated estuarine nursery grounds; and (3) outlined geographic ranges of Tortugas and Sanibel shrimp stocks.

Prior to migrating offshore, the length of time spent by juvenile pink shrimp in the nursery areas varies from about 2 to at least 6 months. In migrating from nursery areas, some shrimp travel at least 150 miles (nautical) before recovery on the offshore grounds. Although migration routes are broad, shrimp emanating from particular sections of the nursery grounds demonstrate distinct distributional patterns on the offshore grounds.

The nursery grounds of the Tortugas shrimp stocks include Florida Bay and estuaries extending at least as far north as Indian Key on the southwest coast of Florida. The nursery grounds of the Sanibel shrimp stocks are confined to the southwest coast of Florida and include estuaries extending at least from Indian Key north to Pine Island Sound.

The geographic ranges of the Tortugas and Sanibel pink shrimp stocks overlap in the nursery areas near Indian Key and in the offshore water between the two trawling grounds. Apparently, Tortugas shrimp do not migrate to the Sanibel grounds and migration from the Sanibel to the Tortugas grounds is minimal. The geographic distributions depicted may constitute minimums for two reasons: First, the absence of fishing effort in certain contiguous areas prevented observations which could extend the known distribution. Second, larval and postlarval pink shrimp may migrate to or from areas beyond the ranges frequented by Tortugas and Sanibel shrimp as juveniles and adults.

The migrations and geographic distribution of pink shrimp, *Penaeus duorarum*, supporting commercial shrimp fisheries on the Tortugas and Sanibel grounds, have not been described previously. These two fisheries, located in the Gulf of Mexico off the southwest coast of Florida, provide a total shrimp catch of about 18 million pounds (heads on) annually. Knowledge of pink shrimp movement and distribution both on and off the grounds will contribute to a more thorough understanding of this animal's biology and serve as a basis for management of this resource.

The catch on the Tortugas and Sanibel grounds consists primarily of maturing and adult pink shrimp. This species has a life history similar to other members of the genus *Penaeus*. As adults, the female pink shrimp extrude eggs in offshore waters. After hatching, the young shrimp pass through larval and into postlarval stages as they move toward the coast. Coastal shallows and estuaries, utilized as nursery grounds, furnish an ecological environment considered necessary for these shrimp during the early stages of their development. The shrimp gradually move off-

[1] Contribution No. 193. Bureau of Commercial Fisheries Biological Laboratory, Galveston, Tex.

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shore while maturing. The larger individuals eventually occupy the deeper waters (Iversen, Jones, and Idyll, 1960).

To study the Tortugas and Sanibel pink shrimp stocks as biological units, we must define the areas supporting these populations (or this population). This definition requires delineation of the shallows and estuaries that sustain young pink shrimp before they migrate to the Tortugas or Sanibel grounds, as well as the deeper, offshore waters frequented by the adult shrimp.

The extensive shallow waters surrounding and penetrating the southern portion of peninsular Florida and the adjoining Florida Keys support an abundance of juvenile pink shrimp, some of which are captured and sold as bait (fig. 1). Florida Bay, lying between the southern tip of Florida and the Florida Keys, is considered an important nursery area supplying pink shrimp to the Tortugas grounds (Iversen and Idyll, 1960). These nursery grounds may extend southwestward into the grassy shallows west of Marquesas Keys (Ingle, Eldred, Jones, and Hutton, 1959). Broad (1950) notes that "ample nursery grounds are to be found on the Florida west coast between Cape Sable and Cape Romano where the coastline is broken by numerous bays, creeks and rivers."

Maturing and adult pink shrimp are found in most offshore waters adjacent to south Florida, sometimes in depths of 60 fathoms [2] (Bureau of Commercial Fisheries, 1961 and 1962). On the Florida shelf, however, much of the bottom is too rough for conventional trawling gear. South of lat. 27°00′ N., the region under discussion, large pink shrimp are generally taken commercially only on the Sanibel, Tortugas, and Hawk Channel grounds where relatively smooth bottom can be found. Pink shrimp are fished commercially to a maximum depth of about 33 fathoms. The greater depths of the Straits of Florida, to the south and east of the Tortugas grounds, and the Gulf of Mexico, to the west, may serve as barriers to the migration of juvenile and adult pink shrimp.

In 1958, a total of 1,157 pink shrimp were tagged with Petersen disks and released near Flamingo in Everglades National Park. From this group, 1 tagged shrimp was recovered on the Tortugas grounds (Iversen and Idyll, 1960). Prior to this recovery no direct evidence linked small pink shrimp from south Florida estuaries to those larger shrimp supporting offshore fisheries. In addition, the relationship of pink shrimp occurring on the Hawk Channel and Sanibel grounds to the Tortugas pink shrimp was unknown. In 1958, the Bureau of Commercial Fisheries began a series of mark-recovery experiments in the waters of south Florida. One result of these experiments has been to demonstrate that certain shallow coastal waters are important contributors of recruits to the Tortugas and Sanibel shrimp fisheries. These experiments also outlined much of the range of the Tortugas and Sanibel pink shrimp stocks.

In studying pink shrimp, we were also concerned with the incidence of similar species that might be mistaken for pink shrimp. Two species closely related to pink shrimp have been reported from the waters of south Florida. These are *Penaeus brasiliensis* (Eldred, 1960) and *Penaeus aztecus* (Burkenroad, 1939; Tabb and Manning, 1961; Bureau of Commercial Fisheries, 1961). In Biscayne Bay and Hawk Channel, a relatively small number of *P. brasiliensis* were marked and released with *P. duorarum*. *P. brasiliensis* has not been noted from the Tortugas or Sanibel grounds despite examination of many shrimp from these areas. Two specimens of *P. aztecus* have been recorded from the northwest portion of the Sanibel grounds, but none from the Tortugas grounds.

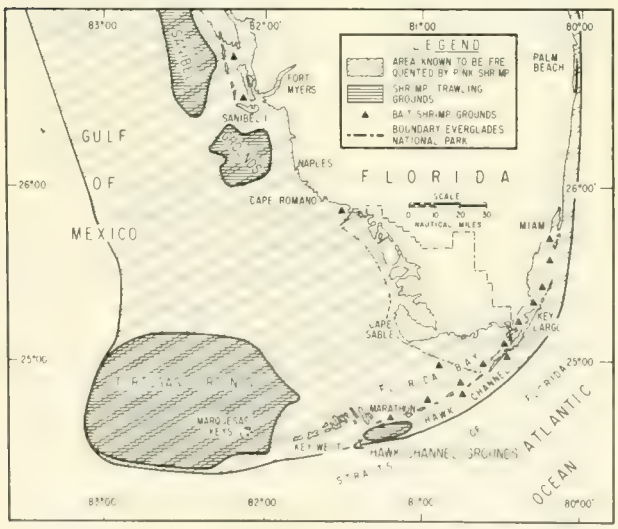

FIGURE 1.—Distribution of pink shrimp in the waters of south Florida.

[2] Off the western edge of the Great Bahama Bank pink shrimp have been found in depths up to 200 fathoms (Bureau of Commercial Fisheries, 1961).

PROCEDURE

Design of Experiments

The experimental plan was based on the assumption that nursery grounds that furnish recruits to Tortugas and Sanibel pink shrimp populations are located in the estuaries and shallow marine waters of south Florida. To delineate these nursery areas and relate them to specific offshore shrimping grounds, young shrimp at selected coastal sites were captured, marked, and released near the point of original capture. Recovery of these marked shrimp on the Tortugas or Sanibel grounds established the affiliation of shrimp from a nursery area to those on the offshore grounds.

Inshore release sites were selected geographically near centers of juvenile shrimp abundance. At several of the selected locations, juvenile pink shrimp are plentiful only seasonally. Therefore, to obtain sufficient shrimp for marking, timing of inshore releases necessarily coincided with these estuarine peaks of abundance. Proceeding with marked shrimp releases according to these criteria, we established the affiliation of shrimp from shallow water areas along an extensive expanse of coastline to the offshore grounds.

Three offshore mark-recovery experiments, designed primarily to determine growth and mortality rates, also furnished information concerning migration and distribution of the larger pink shrimp.

Marked shrimp, which form the basis of this report, were stain-marked by injection of biological stains (Menzel), 1955; Dawson, 1957; Costello, 1964).

Recovery of Stained Shrimp

Shrimp fishermen and packers were informed of the purpose of mark-recovery experiments prior to each release of stain-marked shrimp. Preserved stain-marked shrimp in glass vials were displayed and posters describing stain-marked shrimp were placed in shrimp packing plants. For each recovery, together with the position, date and depth of recapture, rewards of from $1 to $5 were offered at various stages of the program.

Except for four recoveries made by Bureau of Commercial Fisheries vessels, all 2,201 of the marked shrimp recoveries which form the basis of this report were made by commercial fishing vessels. Inshore recoveries were made by bait shrimp fishermen in Biscayne Bay, Barnes Sound, and Florida Bay, and near Indian Key.

Stain-marked shrimp released offshore in or near areas where shrimp trawlers were active were caught and returned for reward payments in surprising numbers. Two groups released on the Tortugas grounds yielded 1,227 recoveries—21.1 percent of the first group released and 33.3 percent of the second group released. On Sanibel, 563 marked shrimp were recovered from a release of 2,496—a 22.5 percent recovery.

Inshore or estuarine releases were usually in localities remote from commercial fishing operations. This is reflected in recovery rates which averaged less than 1 percent of the numbers released.

Recovery rates are affected by factors such as the effective number of marked animals released—the number returned safely and in good condition to the environment from which captured. Also affecting recovery rates are direction of migration, location and amount of fishing effort, and awareness and interest of industry personnel in a position to recover marked shrimp. Some or all of these factors varied during the course of these experiments, and they have been considered in evaluating the data.

MIGRATIONS

Release and Recovery Sites

Table 1 summarizes pink shrimp mark-recovery experiments in south Florida waters from 1958 to 1963. Release sites are numbered in chronological order.

Figure 2 depicts the numbered release sites and general area of recovery of stain-marked shrimp. Arrows joining release and recovery sites do not necessarily indicate routes of migration.

On the southwest coast of Florida, marked juvenile pink shrimp released in large numbers in Pine Island Sound (10) migrated to the south and northwest portions of the Sanibel grounds but not to the Tortugas grounds. A release southeast of Sanibel, at Indian Key (14), resulted in recoveries near Indian Key and on both the Sanibel and Tortugas grounds. On the southwest coast of Florida and in Florida Bay, marked juvenile pink shrimp released near Shark River (6), Flamingo (2), Bottle Key (9), and Peterson Keys (3) were recovered in the Tortugas shrimp fishery. Several shrimp from Bottle Key were also caught in

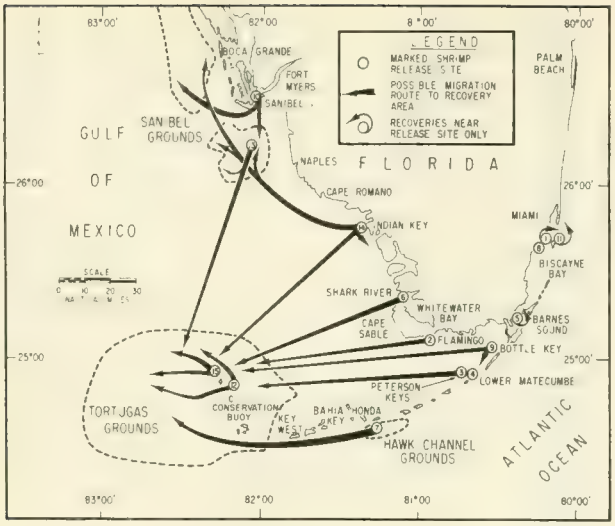

FIGURE 2.—Release-recovery sites of marked pink shrimp in the waters of south Florida, 1958–63.

Florida Bay near and south of their release site, and one was recovered about 6 miles [3] north of the northern border of the Tortugas grounds. A few shrimp released at Bottle Key migrated at least 150 miles to the western portion of the Tortugas grounds.

On the southeast coast of Florida, young shrimp released in Biscayne Bay (1 and 11) and Barnes Sound (5) were recovered only near their respective release sites. No recoveries were reported from one release in Biscayne Bay (8) or from a small release at Lower Matecumbe Key (4), which borders eastern Florida Bay.

Migrations of adult shrimp were determined by releases in the deeper, offshore waters. Although a release of maturing shrimp on the south Sanibel grounds (13) resulted in 561 recoveries in the south Sanibel fishery, only two shrimp migrated to the Tortugas grounds. Marked shrimp released on two separate occasions on the Tortugas grounds near 'C' conservation buoy (12 and 15) apparently remained on or near the Tortugas grounds. The net movement of recovered individuals released on the Tortugas grounds was northwesterly into deeper water. Similar movement has been reported for tagged pink shrimp

[3] Nautical miles are used in this report.

TABLE 1.—*Summary of pink shrimp mark-recovery experiments in south Florida waters, 1958–63*

Release site	Site number	Date of release	Released	Area of recovery	Recovered	Period of recovery	Days-out time [1]		
							Minimum	Maximum	Mean [2]
		1958	*Number*		*Number*		*Number*	*Number*	*Number*
Biscayne Bay	1	Apr. 24–May 29	19,358	Biscayne Bay	57	May–July 1958			[3]
Flamingo	2	Oct. 24–31	7,264	Tortugas grounds	4	Jan.–Feb. 1959	84	121	99
		1959							
Peterson Keys	3	Jan. 29	1,729	Tortugas grounds	11	Mar.–May 1959	46	93	69
Lower Matecumbe Key	4	Mar. 6	1,672		0	No recoveries			
Barnes Sound	5	July 7–16	7,084	Barnes Sound	29	Aug. 1959–Jan. 1960.	16	174	73
Shark River	6	Nov. 2–6	16,638	Tortugas grounds	31	Dec. 1959–Mar. 1960.	35	126	81
		1960							
Hawk Channel	7	Feb. 4	6,815	Tortugas grounds	18	Mar.–May 1960	50	160	83
Biscayne Bay	8	Aug. 9	11,000		0	No recoveries			
Bottle Key	9	Nov. 1–4	13,306	Florida Bay	10	Nov. 1960–Jan. 1961.	22	80	31
				Tortugas grounds	50	Jan.–May 1961	72	205	124
Pine Island Sound	10	Nov. 29–Dec. 15	32,913	S. Sanibel grounds	149	Jan.–Nov. 1961	36	331	106
				NW. Sanibel grounds	6	Mar.–May 1961	112	160	135
		1961							
Biscayne Bay	11	Apr. 18	2,775	Biscayne Bay	4	May–June 1961	34	58	51
Tortugas grounds	12	Sept. 20–23	2,091	Tortugas grounds	443	Sept. –Dec. 1961	1	85	26
		1962							
Sanibel grounds	13	Mar. 19–22	2,496	Sanibel grounds	561	Mar.–Aug. 1962	1	146	33
				Tortugas grounds	2	July 1962	115	115	115
				Indian Key	11	Sept. 1962	7	19	14
Indian Key	14	Aug. 27–Sept. 5	19,860	S. Sanibel grounds	22	Oct. 1962–Apr. 1963.	53	229	159
				NW. Sanibel grounds	1	Nov. 1962	89	89	89
				Tortugas grounds	8	Oct. 1962–Mar. 1963.	40	185	128
Tortugas grounds	15	Dec. 11–15	2,350	Tortugas grounds	784	Dec. 1962–Mar. 1963.	1	106	21
Total			147,351		2,201				

[1] Calculated from the mean release date.
[2] Calculated from all recoveries.
[3] Widespread of release dates at site number 1 negates value of "days-out time" data.

released and recovered on the Tortugas grounds (Iversen and Jones, 1961). Another offshore release of stain-marked shrimp in Hawk Channel (7), south of Bahia Honda Key, yielded recoveries on the Tortugas grounds.

Areal Distribution

In figure 2 lines connecting release and recovery sites suggest possible migration routes traversed by pink shrimp en route to the Tortugas or Sanibel grounds. Actual routes of migration are not known because of the few recoveries in intervening areas which receive limited fishing effort. One exception pertains to the inshore leg of the route followed by shrimp released near Bottle Key as they moved toward the Tortugas grounds. From this group, a bait shrimp fisherman recovered 10 marked shrimp in Florida Bay 22 to 80 days after release. Of these 10, 7 were found near the release site, and 3 had moved southwest of Bottle Key toward a pass breaching the Florida Keys. Higman (1952) reported large catches of shrimp at such passes on night tides flowing from Florida Bay to the Atlantic Ocean. Undoubtedly, many shrimp from Florida Bay move into Hawk Channel, and we have now established that shrimp from the Hawk Channel grounds south of Bahia Honda Key migrate to the Tortugas grounds. Such movement was suggested by Costello and Allen (1960).

The distribution of recoveries from individual releases shows that migration routes may be broad and that shrimp disperse considerably while migrating. For example, shrimp released at Indian Key have been recovered at points as far as 125 miles apart. When there is a protracted departure time from a release site, such as occurred at Bottle Key (table 1), separate elements of the marked group may be subjected to a diverse environment (temperature, salinity, tides, currents) that could affect the direction of migration.

On the Tortugas grounds, the size of pink shrimp increases with the depth (Iversen, Jones, and Idyll, 1960). In general, mark-recovery experiments also indicate that pink shrimp move into deeper water as they increase in size. Thus, from examining the depth contours, we would expect that the majority of recruits enter the Tortugas and Sanibel grounds from the shallower waters northeast, east, or southeast of the grounds. On the Tortugas grounds the recovery patterns of marked

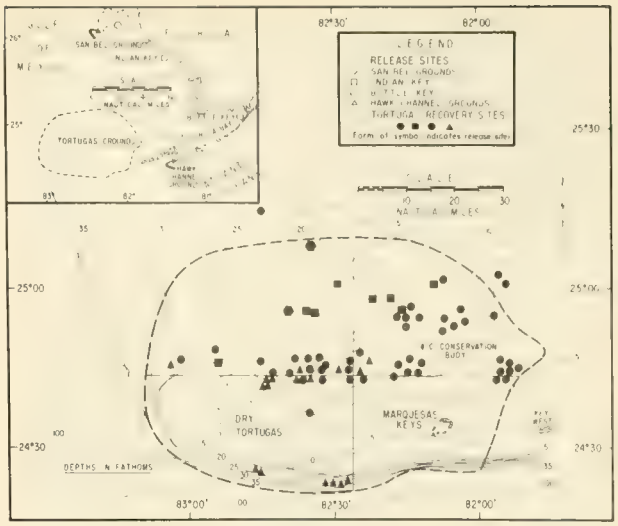

FIGURE 3.—Distribution of recoveries of pink shrimp on the Tortugas grounds from four release sites.

shrimp from a common release area suggest the directions from which the shrimp enter the grounds. Reference is made to figure 3, which illustrates the recovery positions on the Tortugas grounds of shrimp liberated at four release sites Because of varied fishing effort, the actual distributional pattern of marked individuals on the grounds may differ somewhat from that suggested by the recoveries. The greatest concentration of fishing pressure occurs in the northeast quadrant of the grounds followed, in descending order, by the northwest, southwest, and southeast quadrants. Fishing pressure in the southeast quadrant is minimal and probably few recoveries should be expected from there. Bearing these qualifications in mind and by inspecting figures 2 and 3, we made the following observations:

1. Recoveries of shrimp migrating from the Sanibel grounds (13) were confined to the northwest quadrant of the Tortugas grounds, suggesting entrance from the north.

2. Recoveries of shrimp migrating from Indian Key (14) were distributed within the northwest and northeast quadrants of the Tortugas grounds, indicating entrance from the north and northeast.

3. Recovery positions of shrimp migrating from Bottle Key (9) were concentrated in the northeastern and west central portions of the grounds. This recovery pattern may be distorted by the limited fishing effort in the southeast quadrant. Thus, indications are that Bottle

Key shrimp entered the Tortugas grounds from the east, and, perhaps, northeast and southeast.

4. Shrimp that migrated from Hawk Channel (7) were concentrated along the southern border and in the west central section of the Tortugas grounds. Once again, the distributional pattern may be distorted by limited fishing effort in the southeast quadrant. It appears, however, that Hawk Channel shrimp entered the grounds from the southeast.

On the south Sanibel grounds, distribution of the first 23 recoveries of marked shrimp released in Pine Island Sound indicates that these shrimp entered the grounds from the shallower waters to the northeast and east (fig. 4). A comparison of the distributional pattern of the last 23 recoveries with that of the first 23 indicates the general trend of movement was into deeper water, or southwestward on the south Sanibel grounds.

TIME DISTRIBUTION

The period of time expended by pink shrimp (1) on nursery grounds, (2) while traversing migration routes, and (3) on the offshore grounds can be approximated in some cases from the number of days elapsing between release and recovery of marked shrimp, or "days out time" (table 1). Recovery frequencies for half-month periods on the Tortugas and Sanibel grounds (fig. 5) indicate periods of availability of marked shrimp from various release sites. Caution in interpreting these data is necessary since not all shrimp of a marked group depart the release areas at the the same time, are recovered immediately upon reaching the offshore grounds, or are recovered in proportion to their relative abundance.

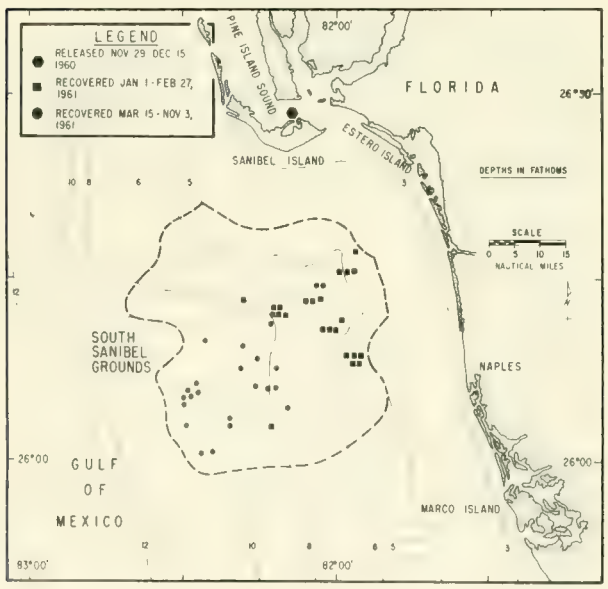

FIGURE 4.—Distribution of recoveries of pink shrimp on the south Sanibel grounds from releases in Pine Island Sound.

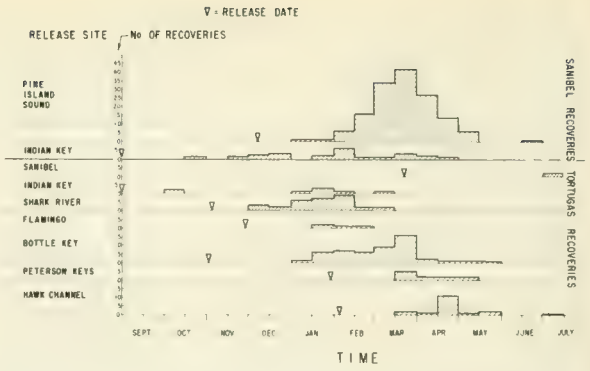

FIGURE 5.—Time-frequency distribution of marked shrimp recoveries on the Tortugas and Sanibel grounds by one-half-month periods.

A few pink shrimp that were marked and released in Barnes Sound (5) remained in the Sound for at least 174 days. Following the pink shrimp age-size relation given by Kutkuhn,[4] we estimated the smallest shrimp released, 16.0 mm. carapace length (75.0 mm. total length), to be about 60 days old. If 21–28 days are allowed for larval and early postlarval development prior to entrance into the nursery grounds, then it appears that under certain conditions more than 6 months of life may be spent in the estuaries. Conversely, time spent in the estuaries may be relatively brief. Only 35 days after the Shark River release (6), one marked male, 20.2 mm. carapace length (94.8 mm. total length), was recovered on the Tortugas grounds. Estimating this shrimp's age as 79 days and subtracting pre-estuarine entrance time, we found it apparently spent less than 2 months in the estuarine environment. The occurrence of pink shrimp less than 20.0 mm. carapace length (92.5 mm. total length) on the Tortugas grounds may indicate that some individuals spent little or no time on the more distant estuarine nursery grounds.

[4] Kutkuhn, Joseph H., Dynamics of a penaeid shrimp population and management implications, p. 313, loc. cit.

Marked shrimp from the Bottle Key release (9), made in November 1960, were recovered in Florida Bay up to 80 days after release. One marked shrimp was recovered in the Bay after two other Bottle Key shrimp had already been caught on the Tortugas grounds. These recoveries show clearly that not all members of a given group of shrimp depart the estuaries at the same time. Bottle Key shrimp were recovered on the Tortugas grounds from January through May 1961 (fig. 5). The majority, however, were taken between January 16 and March 31, indicating that most of the marked Bottle Key shrimp that reached the Tortugas grounds were available for recapture within 75 to 149 days after release. The straight line distance between Bottle Key and 'C' conservation buoy, located near the center of fishing effort on the Tortugas grounds, is about 100 miles. Stained shrimp released in September 1961 (12) and December 1962 (15), near 'C' buoy on the Tortugas grounds, were recovered up to 85 and 106 days after release, respectively. During these periods, many had moved west or northwest into deeper water, some as far as 35 miles. Although several shrimp from release site 15 were taken just south of the northern border of the Tortugas grounds, none was recovered off the Tortugas grounds (fig. 6).

Marked shrimp released in Pine Island Sound (10) in November and December 1960, were recovered on the Sanibel grounds from January through November 1961. The center of the south Sanibel grounds is about 22 miles from the release site. The greatest numbers are recovered between February 1 and May 15. Part of the increase during this period, however, may be a reflection of increased fishing effort. One shrimp was recovered on the Sanibel grounds about 11 months after release. Since the smallest shrimp released was estimated to have been at least 1 month old, the recovered shrimp must have been at least a year old.

Marked pink shrimp released on the south Sanibel grounds (13) in March 1962 were caught there up to 146 days after release. The recovery positions indicated gradual movement into deeper water to the west and southwest. After 115 days two marked shrimp were caught on the northwestern Tortugas grounds, about 80 miles distant.

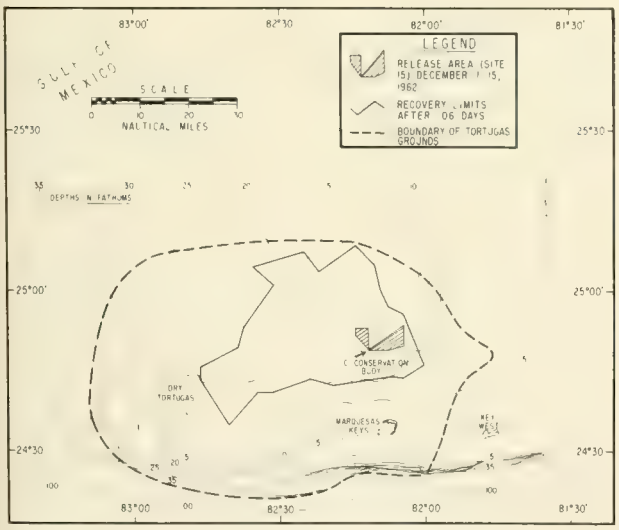

FIGURE 6.—Dispersal of marked pink shrimp on the Tortugas grounds, December 1962 through March 1963.

GEOGRAPHIC RANGE OF THE TORTUGAS AND SANIBEL PINK SHRIMP

The range and relationship of pink shrimp stocks of the Tortugas and Sanibel grounds were demonstrated by mark-recovery experiments. The Tortugas stocks of pink shrimp are defined as those pink shrimp that are available for capture on the Tortugas shrimp trawling grounds during some portion of their life. The Sanibel stocks may be similarly defined by appropriate word substitution. The sources of pink shrimp eggs and larvae that perpetuate these fisheries have not been positively established. Much of the area frequented by Tortugas (or Sanibel) pink shrimp as juveniles and adults, however, can be determined by inspection of marked shrimp release-recovery information (fig. 2 and table 1), Figure 7 is provisional and probably depicts only the minimum ranges of the Tortugas and Sanibel pink shrimp stocks.

Tortugas Stocks

The Tortugas trawling grounds, located northwest, west, and southwest of Key West, have a maximum depth of about 33 fathoms. The "boundary" is rather indefinite and encloses about 3,100 square miles. In much of the area trawling is restricted by rough bottom or extreme shallowness.

North, northeast, and east of the Tortugas grounds, the Tortugas stocks of pink shrimp

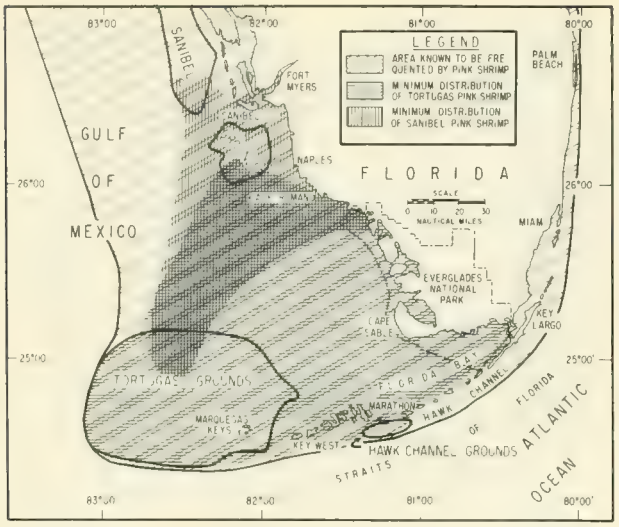

FIGURE 7.—Provisional ranges of Tortugas and south Sanibel pink shrimp stocks.

frequent an area extending at least to release sites 13, 14, 6, 2, 9, 3, and 7 (fig. 2). From the south section of the Sanibel grounds (13), two marked shrimp moved southward to the northwest portion of the Tortugas trawling area, establishing a degree of affiliation between these two fisheries. Because many juvenile shrimp released in Pine Island Sound (10) migrated to the Sanibel shrimp fishery, the relationship of Pine Island Sound shrimp to the Tortugas stocks is also indicated. A total of 35,409 marked shrimp released on Sanibel and in Pine Island Sound, however, yielded 716 recoveries in the Sanibel fishery and only two recoveries to the south, on the Tortugas grounds. Therefore, contribution of shrimp from these two northern sites to the Tortugas fishery must be considered minimal.

Indian Key (14) is about 55 miles southeast of Pine Island Sound. Juvenile pink shrimp from Indian Key are definitely affiliated with the Tortugas stocks, although almost three times as many marked shrimp released at Indian Key were recovered on the Sanibel grounds as on the Tortugas grounds. Analysis of recoveries from release sites 10, 14, and 6 suggests that the northward distribution of Tortugas pink shrimp along the Florida west coast ends north of Indian Key.

Southward from Indian Key to Shark River (6), Flamingo (2), and the Whitewater Bay-Florida Bay complex, we found the northeasterly penetration of the Tortugas pink shrimp stocks restricted by the land mass of the Florida peninsula, not by the coastline. For the Whitewater Bay drainage area, Tabb, Dubrow, and Jones (1962) presented evidence linking juvenile shrimp from estuaries upstream (inland) to the Tortugas population and to coastal release sites proven to be Tortugas affiliated.

The Tortugas pink shrimp recruitment range extends eastward at least to Bottle Key (9) and probably ends at the periphery of northeastern Florida Bay. Evaluation of the results of releases 6, 2, 9, 3, and 7 strongly indicates that all of Florida Bay provides recruits to the Tortugas fishery. Evidence that a separation of stocks may occur between Bottle Key and Barnes Sound (5) is indicated by the fact that considerably more marked shrimp were released in the Tortugas noncontributing areas northeast of Bottle Key than in the adjacent contributing areas to the southwest. A total of 40,217 marked shrimp was released in Biscayne Bay (1, 8, and 11) and Barnes Sound as compared to a total of 15,035 released near Peterson Keys (3) and Bottle Key. Recoveries in Barnes Sound were particularly interesting, because some marked shrimp were recovered near the release site more than 5½ months after release. The Biscayne Bay and Barnes Sound releases, however, occurred in late spring and summer, while the Peterson Keys and Bottle Key releases occurred in late fall and winter. The possibility cannot be discounted that migration patterns and, therefore, stock distribution may vary seasonally. More definitive results might be obtained from releases in both areas during the same season. However, marked shrimp releases at Bottle Key could not be seasonally timed to coincide with the prior release in Barnes Sound because pink shrimp occur in sparse quantities in northeastern Florida Bay during the summer.

The negative results of the Lower Matecumbe Key release (4) can possibly be attributed to a separation of stocks in that area, but are more likely a reflection of the relatively few (1,672) marked individuals released.

In the offshore waters east of the Tortugas grounds, the Tortugas pink shrimp recruitment range extends at least to that part of Hawk Channel (7) south of Bahia Honda Key. However, if shrimp from the Peterson Keys-Bottle Key area are found to use the adjacent Hawk

Channel as a route to the Tortugas grounds (migrations), the known limit of the Tortugas population would be extended northeastward on the Atlantic side of the Keys.

South, southeast, and east of Hawk Channel, pink shrimp have been caught in the Straits of Florida in depths to 60 fathoms (Bureau of Commercial Fisheries, 1961 and 1962). South of the Tortugas trawling grounds, pink shrimp have been taken in depths to 37 fathoms (Springer and Bullis, 1954). At these depths, however, pink shrimp have not been found abundant. The relationship of these "deep water" shrimp to those inhabiting the relatively shallow water of the Tortugas grounds has not been determined.

Sanibel Stocks

The Sanibel grounds comprise two distinct areas of trawlable bottom and are located northwest and south of Sanibel Island. Most trawling is confined to depths of less than 10 fathoms The southern boundary of the south Sanibel grounds is about 50 miles north of the Tortugas northern boundary (fig. 1). The northwest portion of the Sanibel shrimp grounds represents the southern extremity of a sporadic, undefined pink shrimp fishery which parallels a large portion of the Florida west coast.

Recoveries of marked shrimp reveal that Pine Island Sound serves as a nursery ground for both sections of the Sanibel grounds.

In this discussion the two Sanibel areas will be treated separately since there are indications that the northwest Sanibel grounds may support stocks of pink shrimp differing from those of the south Sanibel grounds. This is suggested by the fact that while 2,496 marked shrimp were released on south Sanibel (13), and 563 recovered there, none was recovered on northwest Sanibel despite moderate fishing effort in the latter area. One marked shrimp, however, from the Indian Key release (14) was recovered in the northwest Sanibel fishery. This shrimp very likely passed through the south Sanibel grounds en route to northwest Sanibel, linking all three areas. These apparently contradictory results may indicate that movement of shrimp from the southeast to northwest Sanibel is seasonal or sporadic. Because no marked shrimp have been released on northwest Sanibel, the relationship of shrimp from this area to shrimp stocks to the south is unknown.

The coastal distribution of shrimp recruited to the south Sanibel fishery extends from at least Pine Island Sound (10) to Indian Key (14). Juvenile shrimp recruited to the south Sanibel fishery probably issue from estuaries between and including these release sites. Since 22 of the marked shrimp released at Indian Key were recovered on the south Sanibel grounds, as compared with 8 on the Tortugas grounds, the southeastern limits of the south Sanibel shrimp population probably lie south of Indian Key but north of Shark River. The latter point is emphasized by the fact that releases of 16,638 marked shrimp at Shark River and 23,971 in Florida Bay have resulted in numerous recoveries on the Tortugas grounds but none on the Sanibel grounds.

The distribution of recoveries from coastal and offshore releases provides good evidence that the Tortugas and Sanibel shrimp stocks overlap in the general area of Indian Key (14) and offshore, between the Tortugas and Sanibel grounds. Two stain-marked shrimp, mentioned previously, migrated from the Sanibel to the Tortugas grounds, apparently crossing the intervening area. The bottom in this area is rough and usually precludes successful trawling with conventional shrimping gear. Despite low fishing effort in the area, two pink shrimp tagged and released on the Tortugas grounds were recovered 11 and 14 miles north of the present northern border of the Tortugas grounds (Iversen and Jones, 1961). In addition, one stain-marked shrimp from the Bottle Key release was recovered 6 miles north of the Tortugas border (fig. 3). There is no evidence, however, of migration from the Tortugas to the Sanibel grounds. Of 4,441 stain-marked shrimp released on the Tortugas grounds, none was recovered on or near Sanibel grounds. Because the movement of pink shrimp is generally into deeper water, migration from the Tortugas grounds to the shallower Sanibel grounds seems unlikely.

SUMMARY AND CONCLUSIONS

1. In south Florida, mark-recovery experiments with biological stains as the marking agents demonstrated the importance of certain shallow coastal waters as nursery grounds for pink shrimp that eventually frequent the offshore Tortugas and Sanibel grounds.

2. Some shrimp from shallow coastal waters

migrated at least 150 miles before recovery on the offshore grounds.

3. The recovery patterns show that shrimp disperse considerably between release and recovery, suggesting broad migration routes. Despite such dispersion, shrimp emanating from each nursery area indicated a distinct pattern of distribution on the offshore grounds.

4. Shrimp leaving the estuaries and moving across the offshore grounds tend to move into deeper water. Although limited movement into shallower water was noted on the offshore grounds, such movement is apparently only temporary, because recoveries after long free periods were almost always from deeper water.

5. Mark-recovery data reveal that the length of time spent in the estuaries by shrimp may vary from about 2 to at least 6 months.

6. Between release in an estuary and recovery on an offshore trawling ground the minimum free time of any marked shrimp was 35 days, the maximum 331 days.

7. Shrimp available for capture on the Tortugas trawling grounds emanate from shallower waters to the north, northeast, and east of the grounds. In these directions, the Tortugas stock recruitment range extends at least as far as the south Sanibel grounds, Indian Key, Shark River, Flamingo, Bottle Key, Peterson Keys, and that portion of Hawk Channel south of Bahia Honda Key. Thus, a large portion of the estuarine nursery grounds is located within Everglades National Park. Shallows within the Tortugas grounds may also be a source of recruits to this fishery. The affinity to the Tortugas stocks of pink shrimp occurring in deep water east and south of the Florida Keys, and south, west, and northwest of the Tortugas grounds has not been established.

8. Shrimp available for capture on the south Sanibel trawling grounds emanate from shallower waters along the adjacent coast. Coastally, minimum limits of the recruitment area range from Pine Island Sound, to the north, to Indian Key, southeast of the grounds. Offshore, pink shrimp of the south Sanibel stocks occur on the northwest Sanibel grounds and on the northwestern portion of the Tortugas grounds. The relationship of the south Sanibel pink shrimp to those inhabiting deeper water west of the grounds is not known.

9. The Sanibel and Tortugas stocks overlap along the southwest coast of Florida and in the offshore water between the two trawling grounds. There is evidence that young shrimp recruited from nursery grounds as remote as northeastern Florida Bay and Pine Island Sound associate, as adults, in the area intervening between the Sanibel and Tortugas grounds. Apparently Tortugas shrimp do not migrate to the Sanibel trawling grounds, and south Sanibel shrimp seldom migrate to the Tortugas trawling grounds, or to the northwest Sanibel grounds.

10. The geographic distribution of the Tortugas and Sanibel shrimp stocks as presented here constitutes a minimum range. The absence of fishing effort in certain contiguous regions precluded recoveries and, therefore, identification of these regions as part of the range. In addition, insufficient knowledge of the migrations of larval and postlarval shrimp precludes determination of their origin, which may be beyond the region known to be frequented by the Tortugas and Sanibel shrimp stocks as juveniles and adults.

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TIME OF MIGRATION AND AGE GROUP STRUCTURE OF SOCKEYE SALMON (*ONCORHYNCHUS NERKA*) SPAWNING POPULATIONS IN THE NAKNEK RIVER SYSTEM, ALASKA [1]

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ABSTRACT

The annual sockeye salmon (*Oncorhynchus nerka*) migration to the Naknek River system, Alaska, was studied to determine to what extent major spawning populations were segregated by their time of occurrence in the run. The extent of segregation by age in the run and on the spawning grounds was also studied.

Daily tagging on the Naknek River and subsequent tag recovery on the spawning grounds showed that segregation of individual spawning populations by time of occurrence in the Naknek run is limited. There was a more or less complete intermingling of most spawning groups throughout the run; consequently, most spawning grounds derive their fish from all parts of the run and, generally, in proportion to the size of the daily escapement.

Daily escapement age analysis indicated the lack of marked segregation by age in the Naknek run. No seasonal trend in age was apparent in the 1962 Naknek run.

Differences in age characteristics of major spawning ground populations indicated segregation by age on the spawning grounds of the Naknek River system.

It is generally accepted that sockeye salmon (*Oncorhynchus nerka*), when mature, return to the river system of their origin to spawn. This homing tendency was recognized as early as 1738 (Krasheninnkov, 1754) and given formal expression as the "home-stream" theory in the early 1900's (Chamberlain, 1907). Over a period of many years, evidence in support of this theory was obtained from marking experiments in various river systems from Oregon to Alaska.

The applicability of the "home-stream" theory to individual spawning areas within a river system was first suggested by Gilbert (1914–16, 1918–20) in his investigation of the sockeye salmon of the Fraser River in British Columbia. He found widely differing scale types on fish from different parts of the Fraser River system. Several areas were characterized by spawning populations having scale types so radically different as to permit conclusive segregation of one spawning population from another. Gilbert concluded that the appearance in the fishery of fish with the different scale types could be used to ascertain changes in the racial composition of the catch. Since Gilbert's early work, timing and duration of abundance of various spawning groups have been established by tagging experiments (Thompson, 1945; Killick, 1955), and racial identification has been determined by scale studies (Clutter and Whitesel, 1956; Henry, 1961).

Studies on the Fraser River and several other major sockeye salmon systems in North America have shown that individual spawning populations tend to be segregated in their time of occurrence in the run. Each population appears to have its own specific requirements for survival that govern the time at which it migrates from the sea. For a number of river systems this time seems to

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[1] Based in part on a thesis submitted to the graduate school of the University of Hawaii, Honolulu, in partial fulfillment of the requirements for the degree of Master of Science in Zoology, June 1963.

be related to the distance fish must travel to reach the spawning ground and to the type of spawning area they use. In general, it seems that sockeye salmon with the greatest distances to travel occur in the early part of the run, while those with the shortest distances occur in the late part. This is quite evident on the Fraser River and is reported to occur also on the Copper River in central Alaska.[2]

Segregation of spawning groups in time by the type of spawning area utilized has been reported in some systems.

Barnaby (1944) found that fish occurring early in the run populate all the spawning streams entering Karluk Lake on Kodiak Island, whereas most of those appearing late in the run use only the larger streams and lake beaches. Tagging studies on the Skeena River in British Columbia (Fisheries Research Board of Canada, 1957) indicate that sockeye salmon bound for the smaller tributary streams of Babine Lake pass through the fishery earlier than those bound for the outlet spawning grounds.

Seasonal timing may also be related to the age of fish. Rounsefell (1958) presents evidence that "the age of downstream migration has a negative effect on the season of return. The 2-year migrants run first, followed by the 3-, 4-, and finally the 5-year migrants.[3] The ocean age, on the contrary, has a positive effect. The 4-ocean fish run earliest, followed in succession by the 3-, 1-, and 0-ocean fish groups." [4] Similar changes in age composition during the run were reported for the Copper River by Thompson.

Segregation of age groups of sockeye salmon by lake system and by spawning grounds within a lake system has also been reported in the literature. Although the 4_2 age group [5] dominates the Fraser River run annually, three races—the Chilko, Taseko, and Birkenhead—are characterized by a consistent contribution of the 5_3 age group or "2-year-in-the-lake" fish (Henry, 1961). Koo and Smith (1960) noted that various localities in the Iliamna-Clark system of the Kvichak River drainage in Bristol Bay (fig. 1) showed different age compositions. They stated that this was clear evidence of the segregation of subpopulations. Segregation of spawning groups in time and by age might also occur in the commercially important sockeye salmon runs of other river systems of Bristol Bay.

Knowledge of segregation is basic to understanding the dynamics of sockeye salmon stocks. Further, it would provide information essential in designing studies to identify and determine the abundance of populations in the fishery or in the trunk stream before they disperse to the spawning grounds. Finally, such knowledge would have application in showing whether, and to what extent, individual spawning populations could be managed independently in the fishery and what effect present and contemplated regulatory policies could have on these populations.

The purposes of this study were: (1) To determine the extent that major spawning populations of Naknek sockeye salmon may be segregated by time of occurrence in the run, (2) to determine by age study the seasonal pattern of age distribution, and (3) to determine age segregation on the spawning grounds.

The Naknek River system is one of the major producers of sockeye salmon in Bristol Bay (fig. 1). In some years the sockeye salmon run to the Naknek system has exceeded that to the Kvichak River system, which is generally the most pro-

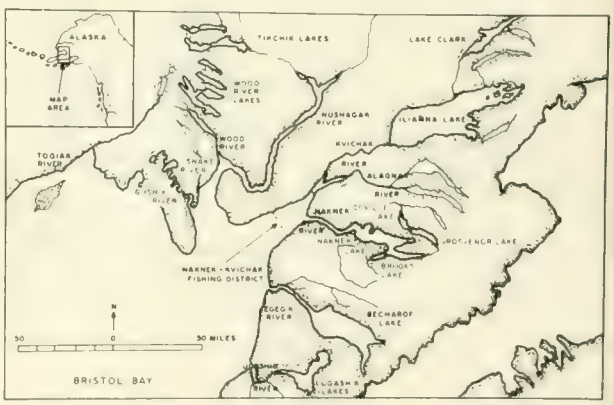

FIGURE 1.—Bristol Bay, showing locations of principal river systems and the Naknek-Kvichak fishing district.

[2] Thompson, Seton H. The red salmon (*Oncorhynchus nerka*) of Copper River, Alaska. Bureau of Commercial Fisheries Biological Laboratory, Auke Bay, Alaska. (Manuscript).

[3] Refers to the age (figured from time of deposition of the egg) at which the juvenile salmon migrates from fresh water to the sea. Thus, a 2-year migrant is a fish that migrates to sea in its second year of life, a 3-year migrant in its third year.

[4] Refers to the number of winters spent in the ocean before the fish returns to fresh water to spawn.

[5] This method of designating the age of Pacific salmon was first introduced by Gilbert and Rich (1927). The first number denotes the total age of the fish (figured from time of egg deposition), and the subscript represents the year of life that it migrated from fresh water to the sea. Thus, a 4_2 salmon, called "four two," refers to a fish that migrated to sea in its second year and returned as an adult in its fourth year of life.

ductive, and has made up most of the Naknek-Kvichak commercial catch. The true size of the Naknek run in any one year is difficult to assess because that portion of the run taken in the commercial fishery intermingles in the Naknek-Kvichak fishing district (fig. 1) with sockeye salmon bound for several of the other rivers entering Bristol Bay. In most years the total catch of sockeye salmon in this district has equaled or exceeded the total spawning escapement to these rivers. Spawning escapements in excess of 2 million have been estimated for the Naknek in recent years, giving some indication of the productivity of this system.

Commercial fishing for sockeye salmon in Bristol Bay is done almost entirely by a gill net fishery which is intense and efficient and capable of taking most of the fish in a district during an open fishing period, essentially eliminating spawning escapement. In the present management of the Naknek stocks the entire run is treated as a homogeneous mixture; therefore, to allow spawning escapement from all parts of the run, the fishery is regulated by periodically opening and closing the Naknek-Kvichak district to fishing.

The spawning grounds of the Naknek River system include a complex of four lakes, Naknek, Brooks, Grosvenor, and Coville, and interconnecting and tributary streams (fig. 2). The annual sockeye salmon migration to the Naknek includes fish destined for interconnecting streams, the tributary stream, and beach spawning areas of all four lakes. Before this study, it was not known if spawning groups could be identified by time of migration.

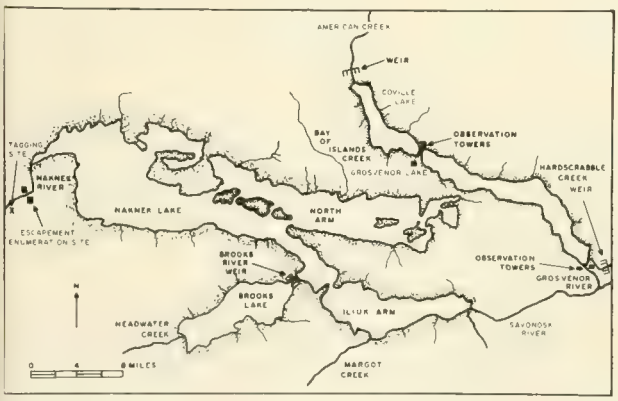

FIGURE 2.—Naknek River system, showing the location of tagging site, weirs, and observation towers.

The Naknek run is of relatively short duration, normally occurring between mid-June and late July, however, spawning takes place over a considerably longer period of time. Depending on the area utilized, spawning may begin as early as late July or as late as early October. The peaks of spawning activity occur about mid-August on the lake tributary streams and during the latter part of September on the interconnecting streams and lake beaches.

Segregation of populations by age groups by time of occurrence in the run and on the spawning grounds has been reported to occur in other river systems, but before this study, little was known of the extent to which this occurred in the Naknek River system.

MATERIALS AND METHODS

Of the various methods now used to identify races of salmon, the tag and recovery technique supplemented by age analysis was considered to be the most direct means for accomplishing the purposes of this study.

TAGGING OPERATIONS

Salmon were captured and tagged daily in 1962 by Bureau of Commercial Fisheries personnel at a site on the south bank of the Naknek River 24 miles above the mouth (fig. 2). Most of the upstream migration in the vicinity of the tagging site occurs along the south bank of the river.

Sockeye salmon ascending the trunk streams characteristically migrate in a narrow band close to shore. Specimens for tagging were caught in a "seine trap" (fig. 3), consisting of a 400- by 12-foot beach seine having 3-inch mesh (stretch measure). The seine was set by boat from shore and attached to a steel stake driven into the river bottom 150 feet offshore. The remaining 250 feet of seine was allowed to trail downstream with the current, forming a partial rectangular enclosure of about 38,000 square feet open on the downstream side. The free end of the net was attached to shore by a rope. The upstream portion of the seine attached to the stake was fitted with a trip lever that could be released by a rope leading to shore. When an observer located in a tower on the river bank saw fish entering the enclosure, the lever was tripped, releasing the net from the stake and allowing it to be carried downstream around the fish. Meanwhile, the free downstream

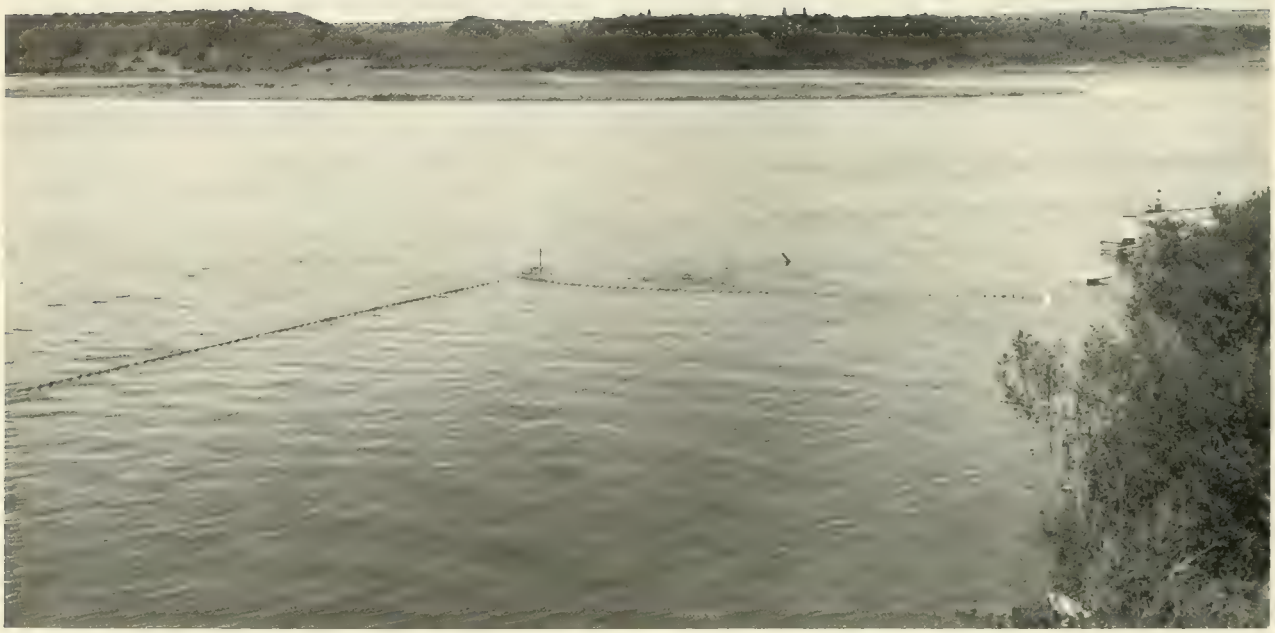

FIGURE 3.—Beach seine trap used to capture sockeye salmon for tagging, Naknek River, 1962. Dock is at right.

end of the net was pulled to shore, completely enclosing the fish.

Three men tagged the fish. The first dipped fish from the holding pen and transferred them to tubs containing an anesthetic; the second transferred the anesthetized fish to the tagging cradle and held it; and the third attached the tag and released the fish.

Two anesthetics were used. From June 24 to 30, tricaine methanesulfonate (MS 222) was used; from July 1 to 18, the remaining period of the experiment, quinaldine was used because of its more rapid action in producing anesthesia.

A pair of 1-inch plastic disk tags was attached to the fish (one on each side) with a nickel pin that was inserted through the fleshy part of the back about 1 inch below the base of the posterior to the insertion of the dorsal fin. A different color combination of tags was used each day (table 1), making it possible to determine the date of tagging through visual observation of tagged fish on the spawning grounds. The tags applied to the left side of the fish were serially numbered.

Between June 24 and July 18, 1962, 6,822 sockeye salmon were tagged (table 1), accounting for 0.94 percent of the estimated total run and giving an estimated tagged to untagged ratio of 1:106.

TAG RECOVERY

Tagged fish recoveries were in the form of both visual observations and actual recaptures. Observations provided information only on the date of tagging. Recaptures yielded additional information on age, length, and sex.

SAMPLING FOR AGE, SIZE, AND SEX

A portion of the fish captured and tagged each day was sampled to determine the age, size, and sex composition of the Naknek spawning escapement. Some fish from every seine haul were sampled, the exact number depending on the size

TABLE 1.—*Sockeye salmon in daily escapements and number and percent tagged, Naknek River, June 24 to July 21, 1962*

Date	Fish in daily escapement [1]	Tag color combination [2]	Fish tagged in daily escapement	
	Number		*Number*	*Percent*
June 24	0	B-G	2	[3]
25	6	W-Y	85	[3]
26	7,122	R-B	31	0.44
27	1,578	G-W	113	7.16
28	1,434	Y-R	6	0.42
29	10,974	B-W	324	2.95
30	74,286	R-G	726	0.98
July 1	20,214	Y-B	109	.54
2	10,956	W-R	144	1.31
3	20,112	G-Y	588	2.92
4	21,666	B-B	525	2.42
5	293,712	R-R	1,704	0.58
6	128,514	Y-W	713	.55
7	115,938	G-G	660	.57
8	6,024	B-Y	178	2.95
9	2,412	W-G	314	13.02
10	1,116	Y-Y	204	18.28
11	1,182	B-R	213	18.02
12	1,194	G-B	106	8.88
13	2,142	R-W	31	1.45
14	954	W-B	25	2.62
15	666	Y-G	11	1.65
16	792		0	
17	372		0	
18 [4]	216	R-Y	10	4.63
19	18			
20	42			
21	24			
Total	723,666		6,822	0.94

[1] Escapement estimates provided by Alaska Department of Fish and Game. Margin of error determined from previous studies is 3 percent of estimated total run.
[2] Colors used were blue (B), green (G), red (R), white (W), and yellow (Y). The first letter of a color combination designates the left side tag color.
[3] Percent of daily escapement tagged was not completed for the first 2 days. The earliest fish to arrive commonly held up between the tagging and tower sites below the rapids for a day or two until the schools build up in size.
[4] Tagging ended on this date.

of the catch and the magnitude of the daily escapement. If the escapement and seine catch were small, every fish was sampled; if they were large, every second, third, or fourth fish was sampled. A total of 3,094 fish, or about 45 percent of the total number tagged, were sampled.

Samples were also taken from individual spawning grounds during the period of spawning activity and from the weirs on Brooks River and American and Hardscrabble Creeks almost daily. In addition, fish obtained during beach seining for tag recovery records were sampled for age, size, and sex. Survey crews covering the smaller tributary streams for tags sampled the spawners in these areas.

Tagged fish were seen near the outlets of all lakes and on some spawning grounds. Observers in towers located on each bank of the river at the outlet of Grosvenor and Coville Lakes (fig. 2) recorded the number of fish and the color combination of all tags seen entering these lakes. At Brooks Lake observers recorded tagged fish as they passed through counting gates of the Brooks River weir (fig. 2). On certain spawning grounds it was necessary to rely largely on observations of tagged fish, because sometimes the fish could not be recaptured. This was particularly true for salmon spawning on Grosvenor Lake beaches and deep swift portions of Grosvenor River and Naknek Lake outlet areas. Here observers counted tagged fish from towers located on boats.

Actual recaptures of tagged fish were obtained from several sources. On Brooks River and American and Hardscrabble Creeks (fig. 2), tagged fish were obtained at weir traps. Tributary and interconnecting streams that were not checked by means of weirs were surveyed for tagged fish on foot or by boat several times during the spawning period. In some of the larger and deeper streams, tagged fish were recaptured by beach seining or by spearing with the use of skin diving and scuba diving techniques.

Total spawning ground recoveries amounted to 1,202 fish, or about 18 percent of those tagged (table 2). An additional 82 tagged fish were sighted, but the color combinations could not be positively identified.

Scales taken from sockeye salmon at the time of spawning have margins that are absorbed to such an extent that only fresh-water age is discernible on a projector. It was necessary to resort to length-frequency distributions of 2- and 3-ocean sockeye salmon derived from fish sampled at the tagging site (1,428 males and 1,621 females) for the assignment of ocean age to each fish sampled on the spawning ground. Approximately 98 percent of the fish in the 1962 escapement spent 2 or 3 years in the ocean. For assignment of ocean age, the dividing line used between fish of 2-ocean and 3-ocean age was 540 mm. for females and 553 mm. for males. Fish shorter than those lengths were considered as 2-ocean, and those longer as 3-ocean. I found no discrepancies between ages assigned to tagged salmon sampled twice—in the trunk stream and on the spawning grounds.

Fish were measured to the nearest millimeter from the center of the eye to the fork of the tail.

The sex of each fish was determined from external characteristics.

METHODS OF ANALYSIS

Seasonal Timing of Spawning Populations

The extent of segregation of individual spawning populations by time of occurrence in the run may

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TABLE 2. *Numbers of tags recovered on spawning grounds—by color combination, date of tagging, and location Naknek River system, 1962*

Location	Tag color combination [1] and number of salmon tagged (in parentheses)																								Total
	B-G (2)	W-Y (85)	R-B (31)	G-W (113)	Y-R (6)	B-W (324)	R-G (726)	Y-B (109)	W-R (144)	G-Y (588)	B-B (525)	R-R (1,704)	Y-W (713)	G-G (660)	B-Y (178)	W-G (314)	Y-Y (204)	B-R (213)	G-B (106)	R-W (31)	W-B (25)	Y-G (11)	R-Y (10)		
	June							July																	
	24	25	26	27	28	29	30	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	18		
Naknek Lake																									
Naknek River lake outlet		2	1			6			3		7	18	7	2	2		3		2		3	2			58
Bay of Islands Creek						1			3	1	3	17	4	1	2	1	5	1	1						40
Margot Creek						4	2	1	1	7	5	22	3	6		2	2	3	1				2		61
Brooks River		1		3		12	8	5	12	21	30	59	29	17	8	5	11	13	11	4	1				250
Grouped lateral streams		2	1				3		2	5	7	12	6	1		1	3	4		1					48
Iliuk Arm Beach												1	1												2
Miscellaneous [2]		1										1	1	1	1										5
Brooks Lake																									
Grouped lateral streams [3]			[1]		[1]	[3]	[2]		[2]	[2]		[5]	[6]		[1]		[3]								[26]
Headwater Creek [3]									[2]			[1]	[2]			[1]						[1]			[7]
Weir count [4]		1	4	4	1	13	20	2	4	12	9	33	25	9	4	4	3	2			2	1	1		154
Savonoski River																									
Dick's Creek							1		1	6		5	1		1										15
Grosvenor Lake																									
Grosvenor-Coville connecting stream				1															1						2
Grouped lateral streams				1		1	1	2	1	3	4	6	5	4	1	3	1	1	1						35
Hardscrabble Creek		2		2		2	8		10	10	20	29	16	7	1	4	5	5	2	1					124
Grosvenor River										2	4	9	7	3		1	1	2	1	1			1		32
Beach spawning area											2	6	2				2								12
Coville Lake																									
American Creek			1	4		11	14	3	10	34	47	94	57	24	5	18	16	12	3	1	2		4		360
Grouped lateral streams												2	2												4
Total		9	7	15	1	50	57	13	47	101	138	314	166	75	25	39	52	43	23	8	8	3	8		1,202

[1] Colors used were blue (B), green (G), red (R), white (W), and yellow (Y). The first letter of a color combination designates the left side tag color.
[2] Location of recovery unknown.
[3] The figures in this entry are placed in brackets because they are included in the Brooks Lake weir counts and have therefore been excluded from the total at the bottom of the column.
[4] Corrected upstream count taken as lake total.

be shown by the number and distribution of color combinations of tagged fish on the spawning grounds. Theoretically, with no segregation the frequency distributions of color combinations occurring on particular spawning grounds should be similar to those of the overall tagged population.

Because of the size and depth of many spawning areas we could not recapture or see all tagged fish present. If the likelihood of recapture or observation were equal for all tag color combinations, spawning ground recoveries should have reflected the relative proportion of tags from each day of tagging. Minor disagreement between actual and expected tag recovery proportions could have occurred as a result of sampling variation and would not necessarily indicate segregation. On the other hand, any substantial disagreement could be taken as a sign of segregation.

Actual tag recoveries were compared with the expected recoveries for major spawning grounds of the Naknek system in two ways: (1) By graphical comparison of the pattern of weighted spawning ground recoveries by day of tagging with the pattern of the daily escapement passing the tagging site, and (2) by statistical comparison using contingency χ^2 analysis (Snedecor, 1956) to test the hypothesis of like tag recovery distributions between spawning areas.

It would have been desirable to tag a given proportion of the run each day so that individual spawning populations would have been tagged in proportion to their daily abundance. This would have made it possible to compare directly the spawning ground recoveries for each day of tagging with the appropriate daily escapement size. This could not be done, however, because the size of the daily escapement, which was counted upstream from the tagging site, was unknown before each day's tagging.[6] Salmon in the escapement were counted daily from observation towers located on each bank of the river 1½ miles upstream from the tagging site (fig. 2). Counting migrating sockeye salmon from towers has been proved a reliable method of assessing the size of daily escapements in Bristol Bay [7] (Becker, 1962).

The number of recoveries was dependent on the number of fish tagged ($r=0.949$, d.f.$=21$, $P(0.001)$), but because a different proportion of the run was tagged each day, recoveries were weighted to make them directly comparable to the daily escapement size. Weighting was accomplished by adjusting the number of fish tagged each day to a standard proportion of the daily escapement. The standard selected was the proportion tagged (0.58 percent) on July 5, the day when the greatest number of fish were tagged (table 1). Weighted spawning ground recoveries for each day's tagging were obtained as follows:

$$W=\frac{0.58A}{X}$$

Where:

W = Weighted recoveries
A = Actual recoveries
0.58 = Proportion of the escapement tagged on day of greatest tagging
X = Proportion of the run tagged on day in question

For any spawning area, the proportion of adjusted recoveries for each day of tagging is thus directly comparable to the daily escapement. I obtained the graphical pattern of tag recoveries for selected spawning areas by plotting the percentage of the total adjusted recoveries by day of tagging and compared this pattern with that of the daily escapement, which was obtained by plotting the percentage of the total escapement on each day of tagging. The amount of disagreement or similarity between the two graphs indicated the extent of segregation.

We recovered adequate tags to make this comparison for most of the known major spawning grounds of the Naknek system; however, for some areas the difficulty encountered in sampling the spawning populations resulted in insufficient recoveries to make comparisons. These included the beach spawning areas of Grosvenor Lake, the tributary streams of the Savonoski River, and a "suspected" beach spawning area in Iliuk Arm of Naknek Lake (fig. 2). For most of the small lateral tributary streams with small spawning escapements, tag recoveries were so few that streams had to be grouped to provide sufficient recoveries for comparison.

Some problems were encountered in identifying tag color combinations. In shallow-water streams

[6] Estimates of the daily escapement size were provided by the Alaska Department of Fish and Game (table 1).

[7] Staff of the Administration of Alaska Commercial Fisheries. 1956. Progress report and recommendations for 1957, 34 pp. [Processed.]

(less than 5 feet deep), most tag color combinations were easily identified, but in deep-water spawning areas (more than 5 feet deep), most observers reported some difficulty in positively identifying green tags and in distinguishing light blue and yellow tags from white. Red tags were identified the most easily in deep water. Thus, the assumption of equal likelihood of observation for all tag color combinations would not hold true for fish in deep water. The degree of efficiency of observing tagged fish in deep water depends on the depth of the water and the tag color combination. Fortunately, most known spawning in the Naknek system takes place in water that is less than 5 feet deep.

In analyzing recoveries for the experiment, I compared the following spawning areas and the escapement in the manner described above.

1. Individual lakes, i.e., Naknek, Brooks, Grosvenor, and Coville. In this comparison the corrected upstream Brooks River weir count of tagged fish was used as the total recoveries for the lake. This was done because few tags were returned from the Brooks Lake tributary streams. The upstream tag count was corrected by deducting tagged fish that moved back downstream through the weir to spawn in Brooks River. For the other lakes, tag recaptures and sightings obtained by all methods (i.e., during stream surveys, at spawning stream weirs, by beach seining, and by skin diving) were totaled for all streams draining into each lake.

2. Individual, large major valley or terminal streams with similar physical characteristics and periods of spawning activity and with recorded escapements in excess of 10,000 fish. These include American, Hardscrabble, Margot, and Bay of Islands Creeks which drain into Coville, Grosvenor, and Naknek Lakes respectively (fig. 2). Headwater Creek, major tributary of Brooks Lake, had too few recoveries for comparison (table 2).

3. Interconnecting streams (Brooks and Grosvenor Rivers).

4. Grouped small lateral tributary streams of all four lakes combined.

5. Naknek River area at the outlet of Naknek Lake.

Recoveries for days or periods of tagging were arranged in contingency tables for comparisons between selected spawning areas, and the proportion of tags in each period was tested for independence by chi-square. Spawning areas compared in this manner were essentially those listed above. In addition, tag recoveries from the small lateral streams of each lake were grouped to provide adequate numbers for testing and were treated as a single spawning unit. Tag recovery proportions for lateral streams of each lake were compared and tested. Comparisons and tests were also made between spawning areas of unlike physical characteristics, escapement records, and spawning periods (i.e., between the large major valley streams, small lateral streams, and interconnecting streams).

For most of the areas compared, tag recoveries from single days of tagging were too few to permit tests of independence on a day-to-day basis, and sufficient recoveries were obtained by combining the recoveries from several continuous days of tagging into a number of periods that included all 23 days of tagging. Tests of independence were thus made on a period-to-period basis.

Tests for segregation were grouped into tagging periods based on the area of spawning. In the lakes, the 23-day tagging experiment was divided into seven tagging periods with 3 days in each period, except the first and last periods, which had 4 days. In the other spawning areas, it was necessary to group the taggings into three periods. These periods were unequal in length because they were based on the daily escapement pattern of the run (table 1). The first period, representing early-run salmon, included recoveries from taggings between June 24 and July 2. This period contained an early peak of abundance, which is usually characteristic of the Naknek sockeye salmon run. This early peak may represent spawning groups that are segregated in time of occurrence and destined for particular spawning areas. The second period representing middle-run fish, which compose most of the escapement, extended from July 3 to 8, inclusive. The third period, representing "tail-of-the-run" fish, included recoveries from July 9 to 18 taggings.

Age Segregation by Time of Occurrence on the Run and on the Spawning Grounds

Segregation of population by age groups by time of occurrence in the run was studied as follows. The percentages of the various age groups in the daily

escapement were determined from scale readings. Percentages for the four dominant age groups (4_2, 5_2, 5_3, and 6_3), which made up 98 percent of the 1962 escapement, were plotted graphically for each day of sampling. This was done for males and females, both separated and combined. The graphs were examined to determine if particular age groups tended to be segregated in certain portions of the run. Similar graphs were prepared for the percentage of salmon that had spent 2 and 3 years in fresh water and 2 and 3 years in the ocean. The 1962 escapement was composed almost entirely (99.8 percent) of fish of 2- and 3-fresh-water age, and 98 percent of 2- and 3-ocean age. These graphs were examined for the extent of segregation by both fresh-water and ocean ages.

Age segregation on the spawning grounds was studied by comparing the age composition of individual spawning ground samples with each other and with age composition of the total escapement. The age composition of the total escapement was derived from the daily percentage age composition, weighted according to the size of the daily escapement. The escapement and spawning ground age compositions were compared on the basis of age group and of fresh-water and ocean ages. Theoretically, with representative sampling of all spawning areas, a lack of segregation by age categories would be shown by close agreement between the total escapement and the individual spawning ground age compositions. Substantial disagreement would indicate segregation.

The frequencies of occurrence of the four age groups (i.e., 4_2, 5_2, 5_3, 6_3) in most of the run were arranged in a contingency table to compare the age compositions of the individual major spawning grounds of the Naknek system. The proportion of fish in each age group was then tested for independence by chi-square. A probability value of less than $P=0.01$ was considered to indicate unlike age compositions between the areas tested and, therefore, segregation by age on the spawning grounds.

RESULTS AND DISCUSSION

Extent of Segregation by Time of Occurrence in the Run

Graphical comparisons of the pattern of weighted recoveries by day of tagging with the pattern of the daily escapement are a somewhat subjective approach to studying the extent of segregation. On the other hand, statistical tests of like tag recovery distributions between spawning areas are objective in nature. Results obtained by both methods were similar.

Results of Graphical Comparisons

Graphical comparisons of the pattern of weighted tag recoveries for individual spawning areas by days of tagging with the pattern of daily escapement to the entire system are presented in figures 4–7.

It is obvious from these comparisons that most of the spawning areas derive their escapement from all portions of the run. In most areas the proportion of tag recoveries appears, in general, to be related to the size of the escapement on the date of tagging. Greater variability between the tag recovery and escapement pattern is apparent for such areas as Bay of Islands and Margot Creeks, Grosvenor River, and Naknek River at

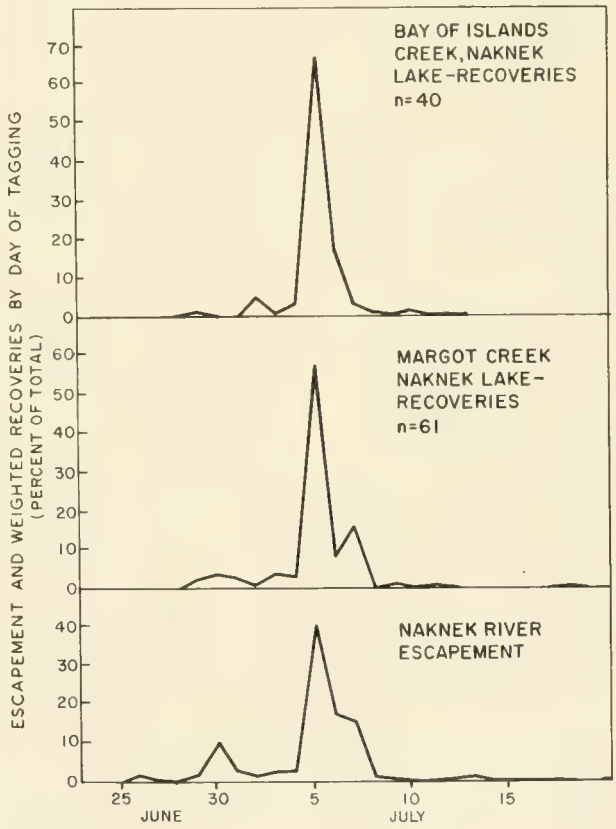

FIGURE 4.—Naknek River escapement and weighted spawning ground tag recovery distributions by day of tagging, 1962 (Margot and Bay of Islands Creeks).

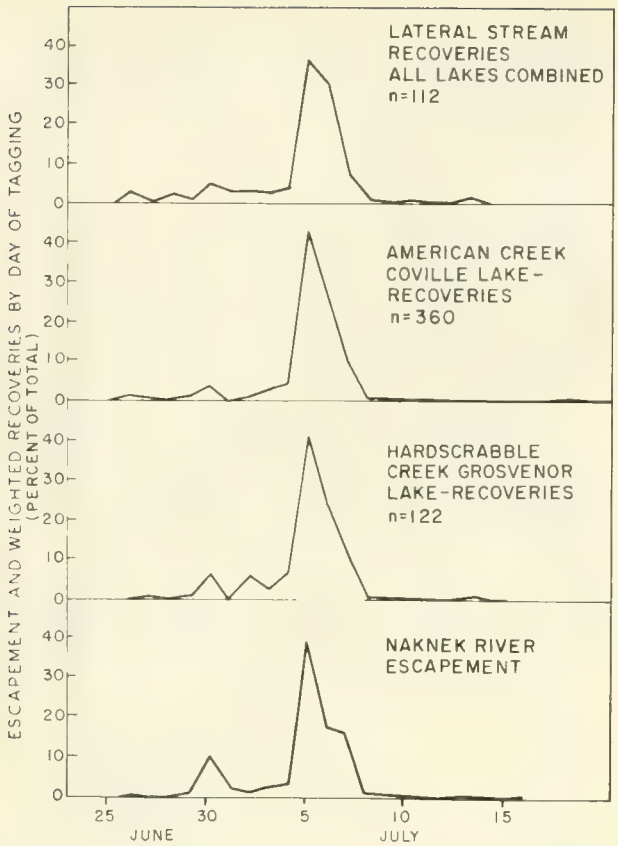

FIGURE 5.—Naknek River escapement and weighted spawning ground tag recovery distributions by day of tagging, 1962 (lateral streams, American Creek, and Hardscrabble Creek).

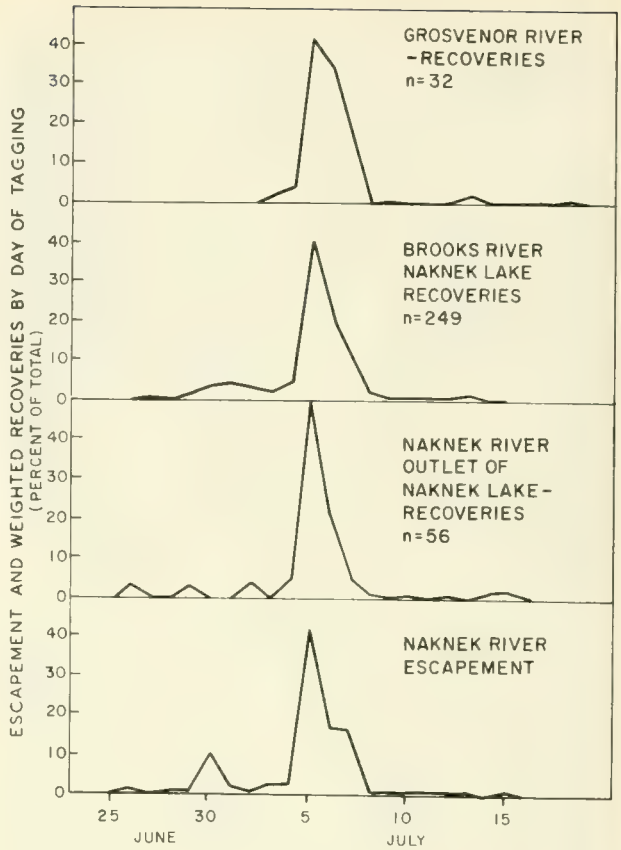

FIGURE 6.—Naknek River escapement and weighted spawning ground tag recovery distributions by day of tagging, 1962 (Naknek River, Brooks River, and Grosvenor River).

the outlet of Naknek Lake (figs. 4 and 6), which had a small number of recoveries (table 2). Spawning areas such as American Creek and Brooks River (figs. 5 and 6), which had a substantial number of recoveries, tend to conform more closely to the daily escapement pattern.

The tag recovery pattern for American Creek (fig. 5) is taken to be representative of the entire escapement into Coville Lake. American Creek, one of the most important spawning areas in the Naknek system, usually receives practically the entire spawning escapement entering Coville Lake. The escapement to the few small lateral streams of Coville Lake in 1962 was only a fraction of that which spawned in American Creek. Only four tags were recovered from these streams (table 2), and they do not change the pattern illustrated by the American Creek recoveries.

The small lateral streams of all lakes had too few tag recoveries for comparison with the escapement on an individual basis; however, the few tags obtained from individual lateral streams were from tags applied throughout the run. When these recoveries are grouped by lakes and weighted in the manner previously described, they provide a pattern quite similar to that of the escapement (fig. 5). The indication is that the escapement to the small lateral streams is also derived from all parts of the run and generally in proportion to the size of the daily escapement.

Two areas, however, seem to show some degree of segregation of their spawning populations. The pattern of recoveries for Brooks Lake shows a greater proportion of tags from the early portion of the run (i.e., before July 2) than the pattern for the other lakes (fig. 7). This is evident not

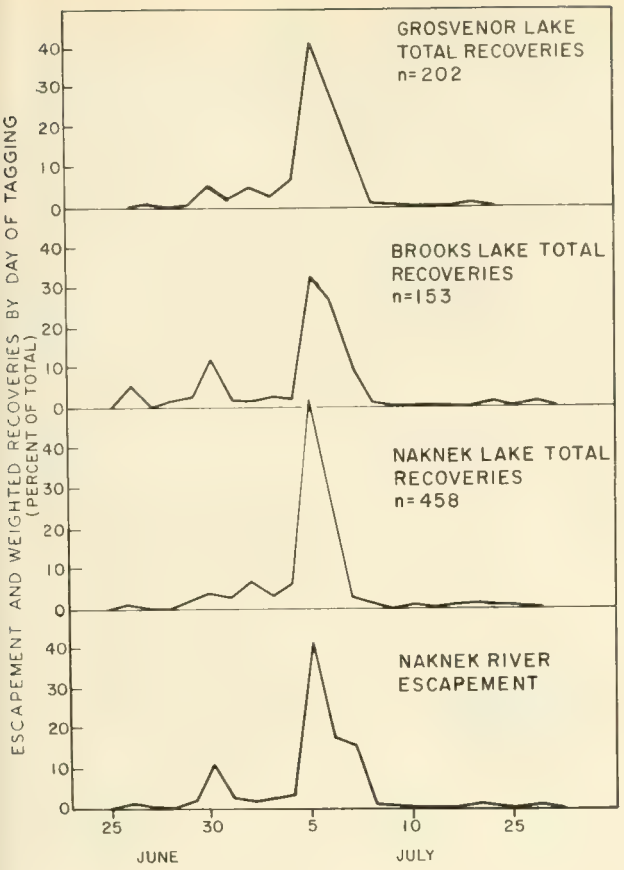

FIGURE 7.—Naknek River escapement and weighted spawning ground tag recovery distributions by day of tagging, 1962 (Grosvenor Lake, Brooks Lake, and Naknek Lake).

only in the Brooks River weir tagged fish count but also in the tag recoveries from the streams tributary to Brooks Lake (table 2).

Grosvenor River had no tagged fish from the early part of the run (fig. 6). Grosvenor River is one of the areas where considerable difficulty was experienced in recapturing tagged fish and in identifying the color combination of those sighted. It is possible, because of the generally smaller numbers of fish tagged in the early part of the run and the few tagged fish recaptured or identified (table 2), that sampling was inadequate and early-run fish were missed as a result of chance. On the other hand, fish from late-run taggings (i.e., after July 2) comparable in size to fish in some early-run taggings were recaptured or sighted in Grosvenor River. This plus the fact that tags were not recovered from the only large tagging day, June 30, in the early part of the run (table 1) strongly suggests segregation of the Grosvenor River population in the latter part of the run. Not enough tags were recovered, however, to formulate a definite conclusion concerning the segregation of the Grosvenor River spawning populations.

Results of Statistical Comparisons

Chi-square tests of the hypothesis of like recovery distributions for comparisons between similar and dissimilar spawning areas yielded results that substantiate those presented above. Probability values less than $P=0.05$ are considered to indicate unlike tag recovery distributions and, therefore, segregation in time of occurrence in the run.

For the comparison between major valley or terminal streams (American, Hardscrabble, Bay of Islands, and Margot Creeks (table 3)), a value of $\chi^2=5.38$, d.f.$=6$, $P=0.50$ was obtained. This high value of P indicates no significant difference between the tag recovery distributions for these streams and, therefore, little segregation of their spawning populations by time of occurrence in the run.

A value of $\chi^2=4.49$, d.f.$=4$, $P=0.37$ was obtained from the comparison of recovery distributions for the grouped lateral streams of Naknek, Brooks, and Grosvenor Lakes (table 4). Coville Lake lateral streams could not be included

TABLE 3.—*Numbers of tags recovered by dates of tagging for major valley streams, Naknek River system, 1962*

Stream	Tags recovered by dates of tagging			Total
	June 24–July 2	July 3–8	July 9–18	
Bay of Islands Creek	4	28	8	40
Margot Creek	8	43	10	61
Hardscrabble Creek	24	83	17	124
American Creek (Coville Lake)	43	261	56	360
Total	79	415	91	585

TABLE 4.—*Numbers of tags recovered by dates of tagging for grouped lateral streams, Naknek River system, 1962*

Lake	Tags recovered by dates of tagging			Total
	June 24–July 2	July 3–8	July 9–18	
Naknek	7	31	9	47
Grosvenor	6	23	6	35
Brooks	9	14	3	26
Total	22	68	18	108

in the comparison because of insufficient tag recoveries. This high value of P indicates a lack of segregation of lateral stream spawning populations by time of occurrence in the run.

The comparison between the total recovery distributions of Naknek, Brooks, Grosvenor, and Coville Lakes (table 5) yielded a P of less than 0.005, suggesting a difference in time occurrence in the run for the populations destined for these lakes. However, almost two-thirds of the chi-square value of 56.57, d.f.=18 is due to the occurrence of a greater than expected proportion of early-run tagged fish in the Brooks Lake escapement (fig. 7). If the Brooks Lake tag recoveries are excluded from consideration and a comparison made only between Naknek, Grosvenor, and Coville Lakes recovery distributions, the resulting $\chi^2=7.43$, d.f.=12, $P=0.82$. Thus, the recovery distributions for these three lakes are not significantly different, and segregation of their spawning populations as a whole is minimal. For Brooks Lake, however, results suggest that it derived a relatively greater proportion of its spawning population from the early part of the run than did the other three lakes.

TABLE 5.—*Numbers of tags recovered by dates of tagging for Naknek, Brooks, Grosvenor, and Coville Lakes, 1962*

Lake	Tags recovered by dates of tagging							Total
	June 24–27	June 28–30	July 1–3	July 4–6	July 7–9	July 10–12	July 13–18	
Naknek	11	36	61	233	50	60	13	464
Brooks	9	34	18	67	17	7	3	155
Grosvenor	5	12	26	110	25	21	3	202
Coville	5	25	47	202	47	35	7	368
Total	30	107	152	612	139	123	26	1,189

Comparison of the tag recovery distributions of unlike spawning grounds, which include the grouped lateral streams of all lakes, Brooks and Grosvenor Rivers (representing interconnecting streams), and American and Hardscrabble Creeks (representing major valley streams) (table 6), yielded a value of $\chi^2=14.87$, d.f.=8, $P=0.06$. This value is essentially at the level of probability ($P=0.05$) below which values of P are considered to indicate unlike tag recovery distributions. The cause of the large χ^2 and resulting low probability level is associated with the absence of early-run (June 24 to July 2) tagged fish in the Grosvenor River recoveries (fig. 6). More than one-third of the χ^2 value of 14.87 is caused by the lack of these early-run tagged fish. Although, statistically, the test does not indicate a tag recovery distribution for Grosvenor River unlike that of the other spawning grounds, the lack of early-run tagged fish in the recoveries and the resulting large chi-square suggest that this area may have derived its escapement primarily from the latter part of the run. If Grosvenor River recoveries are excluded from consideration and a comparison made only between the grouped lateral streams, American Creek, Brooks River, and Hardscrabble Creek, the resulting $\chi^2=8.70$, d.f.=6, $P=0.20$.

TABLE 6.—*Numbers of tags recovered by dates of tagging for unlike spawning grounds, Naknek River system, 1962*

Spawning ground	Tags recovered by dates of tagging			Total
	June 24–July 2	July 3–8	July 9–18	
Grouped lateral streams:				
All lakes	22	68	18	108
Major valley streams:				
American Creek	43	261	56	360
Hardscrabble Creek	24	83	17	124
Interconnecting streams:				
Brooks River	41	164	45	250
Grosvenor River	0	25	7	32
Total	130	601	143	874

Discussion

There is some evidence of heterogeneity between the individual spawning ground tag recovery distributions as compared above. Only Brooks Lake had a tag recovery distribution that differed significantly from those of the other spawning grounds. The distributions for both the lateral streams and the escapement as a whole show that a higher proportion of early-run fish entered Brooks Lake than the other three lakes. Grosvenor River recoveries indicate that it may have received its escapement primarily from the middle and later parts of the run (i.e., after July 2).

Apart from the above situations, however, the evidence presented fails to indicate any clear segregation of most of the known spawning populations composing the Naknek run. It is clear that the recovery distributions for most spawning areas are not significantly different from one another or from the seasonal escapement pattern in the trunk stream. Most areas apparently derive their spawning populations from all parts of the run and, generally, in proportion to the daily escapement.

As mentioned earlier, the Naknek River sockeye salmon run is of relatively short duration when compared with rivers like the Fraser and Karluk. The total spawning escapement enters the Naknek system during a 4- to 6-week period, and normally over half the total escapement occurs in a period of 3 to 5 days (table 1). Spawning activity, however, occurs over a period of 2½ months, although the period and duration of spawning are quite different for the various grounds used. Time of spawning apparently has little effect in producing segregation. Regardless of the characteristics of spawning activity, most grounds seem to receive their escapement proportionately from all parts of the run.

It seems apparent that the short duration of the Naknek run is not an adaptation to a single optimum spawning period for the Naknek system as a whole, and it is probable that the conditions responsible for the compressed nature of the run occur in the ocean before Naknek salmon reach Bristol Bay. Regardless of the cause, it is likely that the short duration of the run is responsible for the significant lack of segregation. The result is, of necessity, a more or less complete intermingling of the spawning populations composing the Naknek sockeye salmon run in the trunk stream and, therefore, in the fishery. In view of this, it seems impossible now to manage in the fishery the individual spawning groups composing the run.

AGE SEGREGATION BY TIME OF OCCURRENCE IN THE RUN

The daily percentages of the four dominant age groups (4_2, 5_2, 5_3, and 6_3) in the 1962 escapement were determined from samples of fish taken at the tagging site. Little difference was noted between the daily age composition of males and females. Both sexes showed similar daily fluctuations in abundance. The age data for males and females were, therefore, combined (fig. 8).

Although daily fluctuations in age composition of the escapement did occur, there were no marked changes in age composition during the run. Only the 5_3 age group appeared to increase in relative abundance toward the end of the run. During the peak escapement period of July 5–7 (table 1), the proportion of the 5_2 age group was somewhat higher and the 5_3 group lower than the overall seasonal average for these groups. Except for daily fluctuations, there appears to be little change

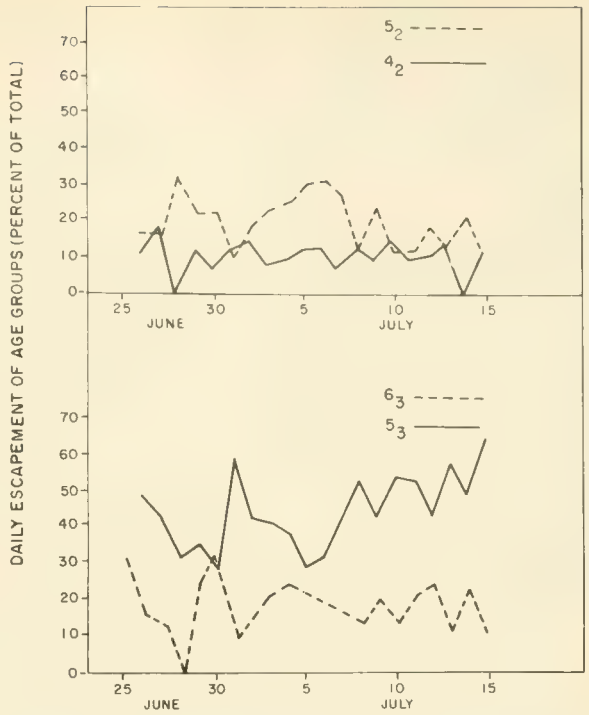

FIGURE 8.—Percent contribution of four dominant age groups of sockeye salmon by day of tagging in Naknek River escapement, 1962.

in the age composition of the escapement with the passage of time. Segregation on the basis of age groups appears to have been minimal in the 1962 Naknek escapement.

In figure 9 the daily age composition of the escapement is replotted by fresh-water and ocean age. When examined from this standpoint, only minor changes in age composition appear to occur during the run. The proportion of 3-fresh-water fish increases, while the 2-fresh-water group decreases slightly after the peak escapement period of July 5–7. Also, the proportion of 3-ocean fish is somewhat higher and that of 2-ocean fish lower during the peak escapement period. There is, however, no marked change in the proportion of any age category during the run. Segregation in time by ocean and fresh-water age appears to have been limited in the 1962 escapement.

To what extent the daily age composition of the Naknek escapement is altered by effects of the fishery is unknown. It is known, however, that the Bristol Bay gill net fishery tends to be selective for the larger or 3-ocean fish (i.e., the 5_2 and 6_3 age groups). It is possible that the fishery could account for the marked day-to-day fluctuations

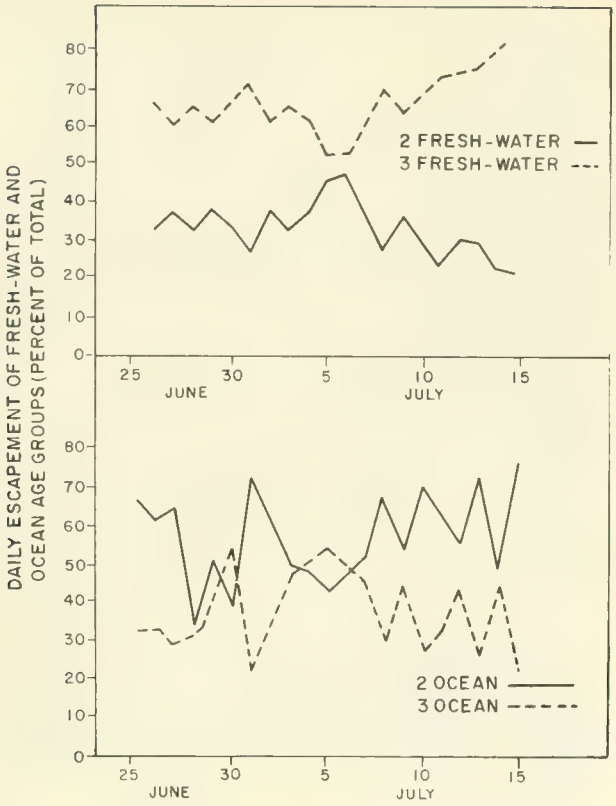

FIGURE 9.—Percent daily age composition of sockeye salmon by fresh-water and ocean age, Naknek River escapement, 1962.

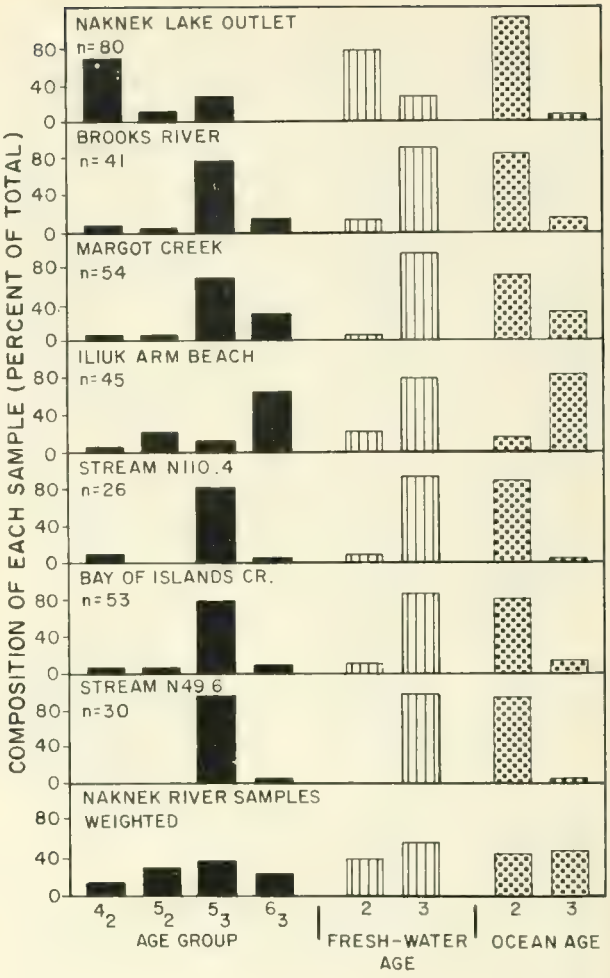

FIGURE 10.—Percent composition of sockeye salmon escapement for major spawning tributaries of Naknek Lake by age group and fresh-water and ocean age, 1962.

that sometimes occur in the age composition and perhaps produce or mask seasonal trends in age.

AGE SEGREGATION ON THE SPAWNING GROUNDS

Results

In figures 10 and 11 and table 7 the age compositions of fish sampled on the spawning grounds are compared with the age compositions of fish sampled at the Naknek River tagging site. In the figures only the individual spawning grounds of each lake with a sample size greater than 25 are compared with the Naknek River samples. Comparisons are made on the basis of dominant age groups (i.e., 4_2, 5_2, 5_3, and 6_3) and fresh-water and ocean age. A complete summary of all age categories present in the samples obtained from all spawning grounds covered in this study is given in table 7.

Figures 10 and 11 and table 7 reveal marked variation in the age composition of the spawning ground samples when compared with each other and with Naknek River samples. This strongly suggests the segregation of populations by age on the spawning grounds of the Naknek River system.

For the major spawning grounds of the Naknek system, the frequencies of occurrence of the four dominant age groups are arranged in a 4–by–9 contingency table (table 8). A chi-square test of the hypothesis of like age compositions for the spawning grounds being compared yielded a value of $\chi^2=549.21$, d.f.$=24$, $P=0.005$. Since the value of P is well below the adopted 0.01 level of significance, it constitutes convincing evidence of unlike age compositions between the areas compared and, therefore, segregation by

TABLE 7.—*Age composition of sockeye salmon on spawning grounds by number and percent, Naknek River system, 1962*

Location	Age group											Fresh-water age			Ocean age			
	3_2	4_2	4_3	5_2	5_3	6_2	6_3	6_4	7_3	7_4	Total	2	3	4	1	2	3	4
Naknek Lake:																		
Stream N 16.1:																		
Number		4	1		3		3				11	4	7		1	7	3	
Percent		36.4	9.1		27.3		27.3					36.4	63.6		9.1	63.6	27.3	
Stream N 18.7:																		
Number		2			3			1			6	2	3	1		6		
Percent		33.3			50.0			16.7				33.3	50.0	16.7		100.0		
Stream N 19.6:																		
Number			1		3			1			5		4	1	1	4		
Percent			20.0		60.0			20.0					80.0	20.0	20.0	80.0		
Stream N 23.4:																		
Number		4			5						9	4	5			9		
Percent		44.4			55.6							44.4	55.6			100.0		
Stream N 49.6:																		
Number					29		1				30		30			29	1	
Percent					96.7		3.3						100.0			96.7	3.3	
Stream N 56.4:																		
Number			1		1						2		2		1	1		
Percent			50.0		50.0								100.0		50.0	50.0		
Bay of Islands Creek:																		
Number		3	1	3	41		5				53	6	47		1	44	8	
Percent		5.7	1.9	5.7	77.4		9.4					11.3	88.7		1.7	83.2	15.1	
Stream N 93.7:																		
Number					20		2				22		22			20	2	
Percent					90.9		9.1						100.0			90.9	9.1	
Stream N 110.4:																		
Number		2	2		21		1				26	2	24		2	23	1	
Percent		7.7	7.7		80.8		3.8					7.7	92.3		7.7	88.5	3.8	
Stream N 111.4:																		
Number				1	6		1				8	1	7			6	2	
Percent				12.5	75.0		12.5					12.5	87.5			75.0	25.0	
Stream N 133.3:																		
Number				1	5		3				9	1	8			5	4	
Percent				16.7	55.6		33.3					11.1	88.9			55.6	44.4	
Iliuk Arm Beach:																		
Number		1		9	6		29				45	10	35			7	38	
Percent		2.3		20.0	13.3		64.4					22.2	77.8			15.6	84.4	
Margot Creek:																		
Number		1		2	36		15				54	3	51			37	17	
Percent		1.9		3.7	66.7		27.8					5.6	94.4			68.5	31.5	
Stream N 142.7:																		
Number		1			5						6	1	5			6		
Percent		16.7			83.3							16.7	83.3			100.0		
Brooks River:																		
Number		3	1	1	30		5	1			41	4	36	1	1	34	6	
Percent		7.3	2.4	2.4	73.2		12.2	2.4				9.8	87.8	2.4	2.5	82.9	14.6	

Location	Age group											Fresh-water age			Ocean age			
	3_1	3_2	4_2	4_3	5_2	5_3	6_2	6_3	6_4	7_3	7_4	Total	2	3	4	1	2	3	4
Naknek Lake:																			
StreamN 156.9:																			
Number			1			2						3	1	2			3		
Percent			33.3			66.7							33.3	66.7			100.0		
Stream N 170.3:																			
Number			1			23						24	1	23			24		
Percent			4.2			95.8							4.2	95.8			100.0		
Lake outlet:																			
Number		1	54		5	20						80	60	20		1	74	5	
Percent		1.3	67.5		6.2	25.0							75.0	25.0		1.3	92.5	6.2	
Brooks Lake:																			
Weir samples:																			
Number	2	4	137	19	183	975	7	107	2	2		1,438	331	1,103	2	23	1,116	290	9
Percent	0.1	0.3	9.5	1.3	12.7	67.8	0.5	7.5	0.1	0.1			23.0	76.7	0.14	1.6	77.6	20.2	0.6
Grosvenor Lake:																			
Lateral streams:																			
Number			4		5	19		8				36	9	27			23	13	
Percent			11.1		13.9	52.8		22.2					25.0	75.0			63.9	36.1	
Lake beaches:																			
Number			6		20	8	1	50				85	27	58			14	70	
Percent			7.1		23.5	9.4	1.2	58.8					31.2	68.2			17.6	82.4	
Hardscrabble Creek:																			
Number			17		19	55		53	1		1	146	36	108	2		73	73	
Percent			11.6		13.0	37.7		36.3	0.7		0.7		24.7	74.0	1.3		50.0	50.0	
Grosvenor River:																			
Number			8		8	30		45	1		2	94	16	75	3		39	55	
Percent			8.5		8.5	31.9		47.9	1.06		2.1		17.0	79.8	3.2		41.5	58.5	
Coville Lake:																			
American River:																			
Number			35	1	193	149	1	295	1	1	1	677	230	446	2	2	185	489	2
Percent			5.2	0.15	28.5	22.0	0.15	43.5	0.15	0.15	0.15		33.9	65.8	0.30	0.30	27.3	72.1	0.3
Naknek River samples weighted: percent		0.1	11.9	0.6	28.7	35.7	1.3	21.4		0.2	0.3		41.9	57.8	0.2	0.7	47.6	50.2	1.5

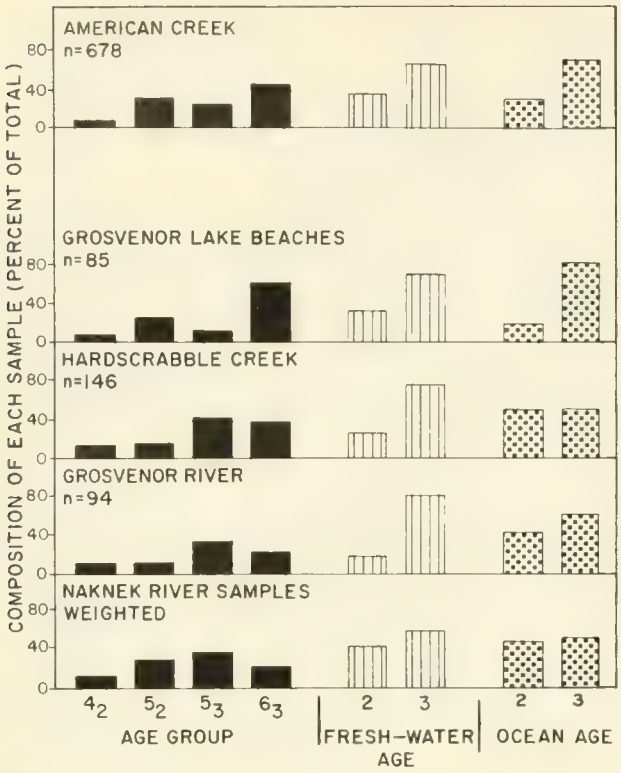

FIGURE 11.—Percent composition of sockeye salmon escapement for American Creek (Coville Lake) and three major spawning areas of Grosvenor Lake compared with overall Naknek system escapement, by age group and fresh-water and ocean age, 1962.

age on the major spawning grounds of the Naknek River system.

Most spawning ground samples contained a considerably higher proportion of the 5_3 age group and a lower proportion of the 5_2 group than did the trunk river samples. Only the Iliuk Arm, Grosvenor Lake beach, and American Creek samples contained a proportion of the 5_2 group approaching that of the river samples. It is notable that the samples from these three areas also contained almost twice the proportion of the 6_3 age group as did the river samples. Ocean-age samples from these three areas were characterized by predominantly 3-ocean fish in 1962. Practically all other spawning ground samples contained predominantly 2-ocean fish, many of them with twice the proportion that occurred in the river samples.

Fresh-water age samples from most areas contained a considerably smaller proportion of 2-fresh-water fish than did the Naknek River samples. Only the samples from stream N23.4 (9 fish) and the sample taken at the outlet of Naknek Lake (80 fish) (table 7) had greater proportions of 2-fresh-water fish. For the Naknek Lake spawning grounds as a whole there was a lack of 2-fresh-water fish, primarily because of the absence of the 5_2 age group.

TABLE 8.—*Numbers of fish in dominant age groups in sockeye salmon samples taken from the major spawning grounds of the Naknek River system, 1962*

Spawning area	Fish in age group—				Total
	4_2	5_2	5_3	6_3	
Bay of Islands Creek	3	3	41	5	52
Iliuk Arm beach	1	9	5	29	45
Margot Creek	1	2	36	15	54
Brooks River	3	1	30	5	39
Naknek Lake outlet	54	5	20	0	79
Grosvenor Lake beach	6	20	8	50	84
Hardscrabble Creek	17	19	55	53	144
Grosvenor River	8	8	30	45	91
American Creek	35	193	149	295	672
Total	128	260	375	497	1,260

Discussion

The absence of the 5_2 age group suggests inadequate sampling of the total Naknek escapement on the spawning grounds. All known spawning grounds were surveyed and sampled in 1962, but only about half of the total escapement counted on the Naknek River could be accounted for on the spawning grounds surveyed. It seems likely that some major spawning areas were not sampled and that these areas could have contained a high proportion of the 5_2 age group that was so prevalent in the river samples.

Until 1962 the Iliuk Arm beach area of Naknek Lake was not regarded as a probable spawning ground. During the 1962 stream surveys in this area, however, survey crews noted large numbers of fish jumping along a 1½- to 2-mile stretch of the southeast shoreline. These fish were present after most of the tributary stream spawning had been completed, but because of the turbid water, we could not definitely establish whether these fish actually spawned in this area nor could we estimate their number. Evidence suggests, however, that they spawned in the beach area. Subsequent sampling of these fish showed that they were composed of a greater proportion of the 5_2 age group than most of the other spawning grounds sampled. It is likely that this population

was sufficiently large to account for a substantial portion of the 5_2 age group represented in the Naknek River samples, but lacking in the samples from the other spawning grounds.

Other probable spawning areas in the Naknek system include the turbid Savonoski River (fig. 2) and most of its clear-water tributary streams and deepwater beach spawning areas as yet unknown. None of these were sampled in 1962.

Regardless of the spawning areas left unsampled, it seems clear from the evidence presented that there is segregation by age on the spawning grounds of the Naknek River system. This agrees with the conclusion reached by Koo and Smith (1960) for various spawning areas of the Kvichak River system in Bristol Bay.

Theoretically this segregation could be of great importance in managing individual spawning populations as they pass through the fishery. If certain spawning grounds are characterized by populations composed predominantly of fish of 2-ocean age and others of 3-ocean age, the effects of the gill net fishery, which is selective for large fish, would be unequal for each group. A knowledge of any consistencies in the age structure of individual spawning populations would, therefore, provide those charged with managing the Naknek sockeye salmon stocks with a means of gaging the possible effects of the fishery on these populations. Many years of data, however, will be required before consistencies in the age structure of individual spawning populations could show up.

The results presented above suggest two important lines of future investigation: (1) A complete survey of all beach and turbid water areas of the Naknek system for spawning areas that were previously undetected, and (2) continued study of segregation by age on the spawning grounds to uncover any consistencies in the age group structure of individual spawning populations.

SUMMARY

1. Tag and recovery techniques were used to determine the extent of segregation by time of occurrence for the individual spawning populations in the sockeye salmon run of Naknek River, Alaska. Salmon were tagged daily on the Naknek River at a site located about 24 miles above the mouth of the river. A different tag color combination was used to identify each day of tagging. Subsequent recovery or observations of tagged fish on the spawning grounds and the relative abundance of each color combination present provided the basis for determining the extent of segregation.

2. Results lead to the following conclusions: (*a*) Segregation of individual Naknek spawning populations by the time of occurrence in the trunk stream was minimal. As a consequence, most spawning grounds derived their fish from all parts of the run and, generally, in proportion to the size of the daily escapement. Exceptions were Brooks River, which received a disproportionate share of early-run spawners, and Grosvenor River, which seemed lacking in early-run fish. (*b*) The short duration of the Naknek run is probably the most reasonable explanation for the intermingling of most spawning groups. (*c*) Because of the lack of segregation in time, it is unlikely that spawning populations can be managed on an individual basis in the fishery. The Naknek sockeye salmon stocks will probably be most effectively managed, as a whole, by securing spawning escapement proportional to the daily abundance of fish in the fishery.

3. No seasonal trends in age composition could be described as characteristic of the Naknek run, probably because of intermingling of most of the spawning populations during the run.

4. Fish from all known spawning grounds of the Naknek system were sampled to determine the age composition of populations associated with the separate spawning areas. Spawning populations have age characteristics that differ significantly from one to another and, therefore, show segregation by age on the spawning grounds of the Naknek River system. Continued study of segregation by age on the spawning grounds is necessary for a number of years to determine if the age structure of specific spawning populations conforms to specific patterns. It is likely that major spawning population's as yet undetected and, therefore, not sampled in this experiment exist in the Naknek system. A thorough survey to locate and determine the magnitude and age characteristics of these populations, if any, is needed for a complete understanding of segregation and the productive importance of individual spawning areas within the Naknek system.

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SKIPJACK TUNA SPAWNING IN THE MARQUESAS ISLANDS AND TUAMOTU ARCHIPELAGO

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ABSTRACT

Spawning of skipjack tuna (*Katsuwonus pelamis*) in the Marquesas and Tuamotu areas was investigated by examining ova from 402 pairs of ovaries collected during exploratory fishing cruises, August 1956 to June 1958. Investigated were size at first spawning, spawning season, frequency of spawning, fecundity, use of the gonad index as a measure of maturity of skipjack, and the relation of stage of sexual development to schooling behavior.

The length at first spawning of skipjack in the two areas was found to be about 43 cm., although a few fish as large as 50.7 cm. apparently were not yet ready to spawn. Spawning activity reached a peak during November–April. The data indicate a possibility that individual skipjack may spawn more than once during a season. Number of ova extruded per spawning was estimated at 0.1 to 2 million. The gonad index could not be used as a measure of sexual development. Skipjack schools tended to have fish in a similar stage of sexual development.

From 1956 to 1959 the staff of the Bureau of Commercial Fisheries Biological Laboratory at Honolulu investigated the tuna resources of waters of French Oceania around the Marquesas Islands and the Tuamotu Archipelago. A study of the spawning of the skipjack tuna, *Katsuwonus pelamis* (Linnaeus), which appears to be the most abundant surface-schooling species of tuna in this area, was included in the investigations.

This study is based on the systematic microscopic examination and measurement of the ova in skipjack ovaries, generally following the method described by Clark (1934). Skipjack spawning studies, based generally on the examination of gonads or on the capture of larvae and juveniles, have been made in many different areas of the Pacific. On the basis of the examination of gonads, Matsui (1942) inferred that skipjack may spawn throughout the year in the vicinity of Palau; Marr (1948) concluded that spawning occurs in the northern Marshall Islands, and confirmed this by the capture of two juveniles; Yabe (1954) and Yao (1955) found evidence of spawning in the southern waters of Japan; Brock (1954) postulated that they spawn in Hawaii from late February, March, or April to the first part of September; Schaefer and Orange (1956) and Orange (1961) hypothesized that they spawn in the vicinity of the Revilla Gigedo Islands in the eastern Pacific; and Wade (1950a) found evidence of their spawning in Philippine waters.

By virtue of the capture of larvae and juveniles, Schaefer and Marr (1948) demonstrated the existence of a spawning ground off Central America; Wade (1950b and 1951) found further evidence that skipjack spawn in Philippine waters; Shimada (1951) deduced that spawning occurs around the Phoenix Islands; and Matsumoto (1958) showed that they spawn in a wide area in the central Pacific Ocean. The present study demonstrates the existence of yet another spawning locality in the Pacific.

Note.—Approved for publication Oct. 22, 1964.

MATERIALS AND METHOD

COLLECTION OF OVARIES

This study is based on 402 pairs of ovaries collected on seven exploratory fishing cruises from August 1956 through June 1958. The approximate locales of collection are shown in figure 1. Most of the ovaries were collected from fish caught at the surface by pole and line. This method of fishing, as used in the Hawaiian skipjack fishery, was described by June (1951).

Plans for all of the pole-and-line fishing cruises called for sampling 25 skipjack from each school fished in order to obtain an estimate of their size and sex composition. From the 25 fish thus selected, the first 5 females picked at random were cut open and their ovaries removed for examination. Skipjack were caught by pole and line from 92 schools during this study, and ovary samples were secured from fish from 81 of these schools. Longline fishing and incidental trolling provided the few remaining samples. A description of the longline fishing method was given by Mann (1955).

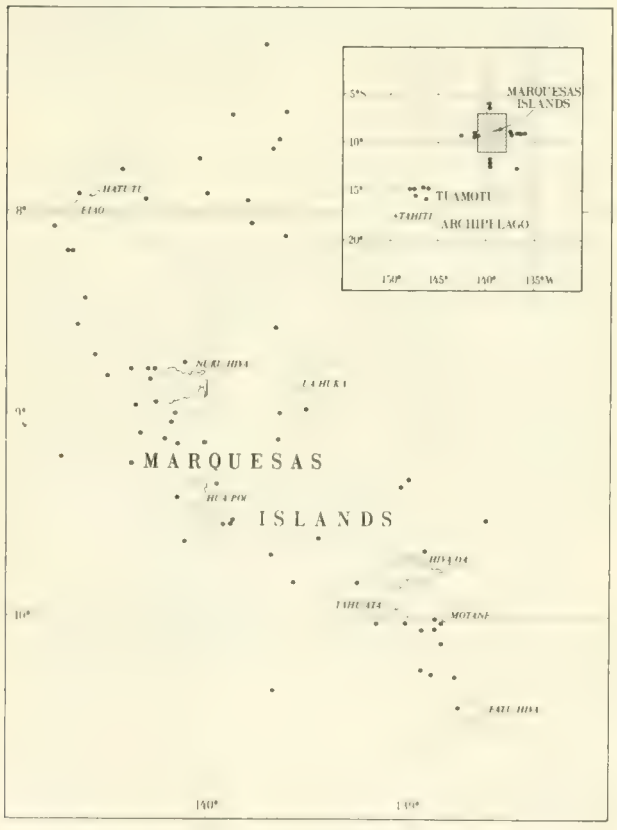

FIGURE 1.—Locations where skipjack ovaries used in this study were collected.

The ovaries were preserved in about 10 percent formalin. At the time of collection a record was made of the date, locality, method of fishing, and the fork length of the fish.

EXAMINATION OF OVARIES

Several investigators made detailed studies of the distribution of mature ova within ovaries: June (1953) for yellowfin (*Thunnus albacares*); Yuen (1955) for bigeye (*Thunnus obesus*); and Otsu and Uchida (1959) for albacore (*Thunnus alalunga*). All showed that a representative sample of ova could be obtained anywhere along the length of an ovary or from either member of a pair.

Similarly, an analysis of variance of the mean size of mature ova within a skipjack ovary indicated that they were homogeneously distributed. Therefore, the following sampling method was adopted for this study. The formalin-preserved ovaries were weighed after excess moisture and tissue had been removed. A cross-section about ⅛-inch thick was taken, usually from the middle of the right ovary, from which a wedge-shaped (triangular) sample was cut. In many instances it was not possible to distinguish the right ovary from the left. In these instances the smaller of the pair was selected for examination; it appeared that the right ovary was usually the smaller of the two. I assumed that the distribution of ova within the right and left ovaries is similar, as has been reported for the tuna cited above.

The ova from the triangular section were teased apart in a shallow dish and measured in a Sedgwick-Rafter counting chamber. Measurements were made with an ocular micrometer having a magnification of 0.016 mm. per micrometer division. Since the ova were not perfectly spherical, the diameter which was measured was the random diameter that fell parallel to the lines in the counting chamber.

At the outset of the study, 300 randomly selected ova, 10 micrometer divisions (0.16 mm.) or larger, were measured from each ovary in order to characterize the size of ova at the different developmental stages. Since this required a great amount of time, and since the determinations of the stage of development of the ovaries were based on the most developed ova, the sample size

was later reduced to a random sample of 25 of the most developed group. Following Snedecor (1946, p. 457), I analyzed the data on ova size distributions; my analysis showed that 25 was an adequate number to approximate the mean size.

DEVELOPMENTAL STAGES OF OVA

Four rather distinct developmental stages were recognized and designated as "early developing," "developing," "advanced," and "ripe". The early developing category includes ova which, at their most primitive, appear as simple transparent cells present in all ovaries. The larger ova in this stage contained a relatively large nucleus. The mean diameter of the early developing ova ranged from 0.16 to 0.33 mm. The ova assigned to the developing stage were completely opaque because of the deposition of yolk granules. Their mean diameter was 0.37 to 0.66 mm. The advanced stage comprised ova that were still relatively opaque in appearance and contained a cluster of small oil droplets to ova that were semitransparent and had a well-developed, bright yellow oil globule. The mean diameter of these ova was 0.49 to 0.74 mm. The collection had no ripe ovaries; however, a sample of ova from a running ripe skipjack caught on January 26, 1957, was available for examination. This skipjack was caught by pole and line at 9°33′ S., 139°55′ W., about 10 miles southeast of the island of Hua Pou in the Marquesas. Its ova were used in an unsuccessful attempt at artificial fertilization and were preserved and brought to the laboratory. They are almost perfectly spherical and transparent, with a distinct straw-colored oil globule. Fifty were measured. Their diameters were 0.85 to 1.12 mm., with a mean of 0.96 mm. The oil globule was about 0.14 mm. in diameter.

The sizes of these ripe ova are similar to those described by other investigators. Brock (1954) found ripe ova from a skipjack in Hawaii to average 1.125 mm. in diameter. Yabe (1954) measured some ova from a ripe skipjack caught in the southern waters of Japan and found that they were 0.80 to 1.17 mm. in diameter, averaging 1.00 mm.

DEGREE OF MATURITY

Skipjack were classified according to the stage of development of the most developed group of ova: the nomenclature used was the same as for the stages of ova development. Throughout this report, unless otherwise stated, the designations early developing, developing, advanced, and ripe will be used interchangeably to describe a skipjack, its ovaries, and the most developed ova contained therein.

The early developing category included ovaries as small as 2 g., from a sexually immature fish, and those (from adult fish) which were relatively large but which contained only early developing and a few residual ova. This category also included some ovaries containing ova that appeared to have attained the developing stage but had begun to degenerate. These ova were grayish, relatively soft, and easily broken.

TREATMENT OF DATA

Skipjack from the Marquesas and the Tuamotu areas were considered together in all aspects of this study, because I assumed that they belonged to the same population or at least were similar physiologically insofar as spawning was concerned. It would have been interesting to determine whether skipjack from the two areas did indeed have similar spawning habits; however, the samples from the Tuamotus were too few to treat that area separately. Of the 402 pairs of ovaries collected, 372 came from around the Marquesas and 30 from the Tuamotus.

SIZE AT FIRST SPAWNING

The approximate body length at first spawning was determined by arranging the lengths and the stage of development of all the skipjack used in this study into a frequency distribution (fig. 2). The smallest skipjack measured 39 cm. This fish had thin, ribbonlike ovaries which weighed 2 g. and contained only primitive ova. Presumably it had never spawned. The ovaries of a few fish, 43.7 to 50.7 cm. long, were classified as early developing and also showed no positive evidence of past spawning. A greater number in that size range, however, had either developing or advanced ovaries. The smallest fish that had advanced or developing ovaries was 43 cm. long. The few fish more than 55 cm. long that were classified as early developing either showed evidence of past spawning or at least of having attained a stage of development past early developing, for their ovaries contained residual or degenerating ova.

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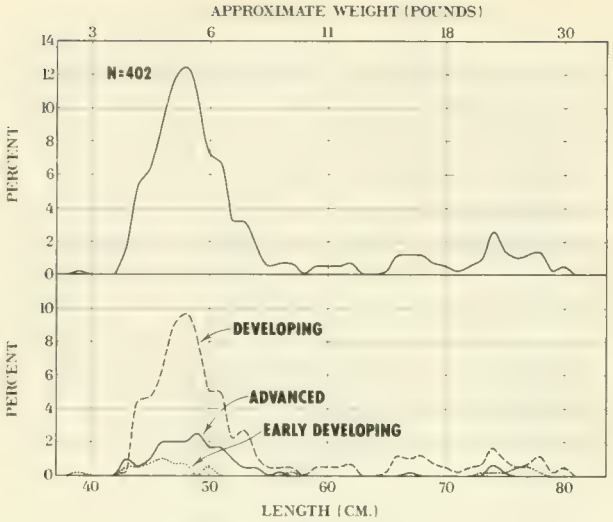

FIGURE 2.—Skipjack length-frequency distribution and stage of development.

It was noted earlier that one skipjack with running ripe ovaries had been caught. Unfortunately, the length of this specimen was not recorded. However, a sample from the school from which this fish was taken showed their size to range from 45.6 to 56.9 cm., and in all likelihood this specimen fell within this length range.

It seems from these observations that, although some skipjack as large as 50.7 cm. were apparently not ready to spawn, those in the Marquesas-Tuamotu areas are capable of first spawning when they are about 43 cm. long.

The size at first spawning has been determined for skipjack in other areas of the Pacific. Brock (1954, p. 102), discussing skipjack in Hawaii, states, "The smallest fish that possessed maturing ova during the spawning season were around 40 to 45 cm. long. Fish 35 to 40 cm. in length had ovaries that, with a few exceptions, seemed immature." In the southern waters of Japan, Yabe (1954) noted that no definite information was available because of the scarcity of data, but that the smallest skipjack in his samples with mature ova was 46.8 cm. long. In the eastern Pacific, Orange (1961) found the minimum size at first spawning for skipjack around the Revilla Gigedo Islands to be about 55 cm., and around the Cocos Island area about 40 cm.

From the above discussion it appears that the size at first spawning may vary with locality. Skipjack in the Marquesas and Tuamotus, in Hawaii, and in the southern waters of Japan all seem to mature at about the same size, while in certain areas in the eastern Pacific they attain a larger size before reaching maturity.

It is interesting that all samples from the Marquesas and Tuamotus were composed primarily of adult fish. The Hawaiian summer skipjack fishery also exploits mostly adult fish (Brock, 1954, fig. 1). In the eastern Pacific, if the size-frequency samples presented by Hennemuth (1957) are typical, the fishery depends on both juvenile and adult fish. The Japanese skipjack fishery probably exploits adult as well as juvenile fish (Yabe, 1954; Yao, 1955).

SPAWNING SEASON

It would be relatively simple to determine the spawning season of skipjack if all the ovaries ripened at the same time and if ripe fish were readily taken. Small numbers then could be examined to follow the development of ova to the time of spawning. My data show, however, the presence of a diversity of developmental stages in any one period; therefore, another method had to be employed to define the spawning season.

The temporal distribution of skipjack possessing ripe or advanced ovaries should give some indication of the spawning season, the implication being that these fish are actively spawning or very close to spawning. The percentage distribution of skipjack by month of capture and stage of development is presented in figure 3. Only those larger than the size at first spawning, and therefore, presumably only adult fish, were used in this analysis. All but one specimen in my collection

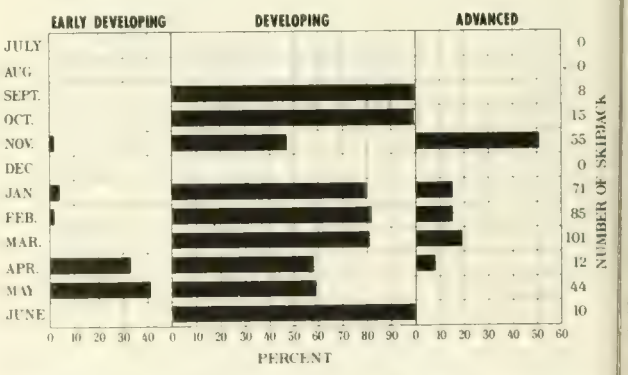

FIGURE 3.—Seasonal distribution of early developing, developing, and advanced skipjack.

were included. As indicated earlier, aside from one running ripe fish, which was caught in January 1957, no ripe skipjack were available during the periods of sampling. Those in the advanced stage were found, however, in November, and January to April. This suggests that their major spawning season in this area is from about November through April.

The spawning season may be further defined by determining the temporal distribution of nonspawning; i.e., early developing skipjack. It was noted earlier that some classified as early developing possessed ovaries that either (1) contained only early developing ova, aside from a few residual ova from a previous spawning, or (2) contained ova that had reached the developing stage but were apparently degenerating. These observations suggest that during certain periods of the year the ovaries may revert to a dormant or early developing stage. A few skipjack classified as early developing were found in November, January, and February; however, the greatest numbers occurred in April and May, the months in which fish in the advanced stage were declining in number or were totally absent. I assumed that such a distribution of early developing and advanced skipjack indicated a decrease in spawning activity during these 2 months. However, the situation is probably more complex, since skipjack in all stages of development were found simultaneously, and fish with developing ovaries were found in all months sampled. In all probability, scattered spawning occurs throughout the year, but the peak activity is from November through April (or, roughly, the Southern Hemisphere summer). The results of a study of the distribution of skipjack larvae in this area, described by Nakamura and Matsumoto,[1] substantiate this conclusion. The larvae were caught in greater abundance contemporaneously with the greatest numbers of fish with advanced ovaries.

Skipjack spawning seasons in other areas, as in Hawaii, appear to be typically long. The season in Hawaii extends from late February, March, or April to the first part of September (Brock, 1954). Schaefer and Orange (1956) indicated that skipjack spawn in the vicinity of the Revilla Gigedo Islands from April to December, and that spawning is more intense in summer and fall. Concerning the fish in the Philippines, Wade (1951, p. 469) states, ". . . there are indications that the period from September to April, inclusive, may be the principal spawning period." The spawning season in the southern waters of Japan, however, is relatively short. Yao (1955) postulated that skipjack spawn during June–August in the waters south of Kyushu and the Ogasawara area.

FREQUENCY OF SPAWNING

The presence of two or more modes in ova-size frequency distributions and that of residual ova in ovaries containing mature ova have been used to hypothesize multiple spawning. Among investigators studying tuna, June (1953) concluded on the basis of such evidence that yellowfin in Hawaiian waters spawn more than once during a season. So did Brock (1954) for Hawaiian skipjack, Yuen (1955) for the bigeye in the Pacific, and Otsu and Uchida (1959) for the Pacific albacore.

The ova-diameter frequency distributions for skipjack in northeastern French Oceania were typically bimodal, or sometimes multimodal in the more advanced ovaries (fig. 4). Furthermore, residual ova were found in ovaries of 23 of the 72 skipjack that were judged to be in the advanced stage.

MacGregor (1957) discussed this problem of multiple spawning in some detail in an analysis of Pacific sardine fecundity. He disagreed with several criteria that have been used in the past to

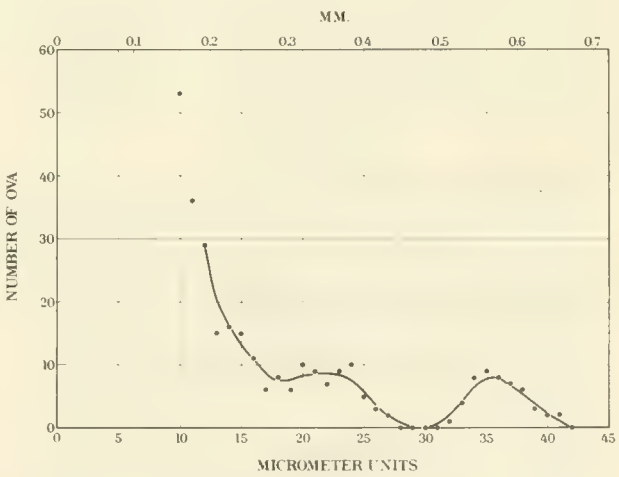

FIGURE 4.—Ova-diameter distribution for a developing skipjack ovary.

[1] Nakamura, E. L. and W. M. Matsumoto. MS. Distribution of larval tuna in Marquesan waters. Bureau of Commercial Fisheries Biological Laboratory, Honolulu, Hawaii. (Manuscript.)

hypothesize multiple spawning; he objected to the criterion of the presence of two or more modes in ova-size frequency distributions. He pointed out that the presence of two or more such modes in developing ovaries does not necessarily mean that all the groups mature and that multiple spawning will occur.

Support for MacGregor's contention may be found in Yabe's (1954) work on skipjack in Japanese waters. He noted that skipjack smaller than 47 cm. had relatively large ovaries from June to August, but that the relative size of the ovaries decreased after September. He suggested that the ovaries shrank without spawning having occurred.

As noted earlier, my data also show some ovaries that were classified as developing but contained what appeared to be degenerating ova; this finding, one may argue, is in agreement with MacGregor's thesis. It also may be argued, however, that these data merely indicate that there may be a cessation of spawning during part of the year and do not necessarily indicate that none of the intermediate-sized ova will be spawned. Furthermore, skipjack as small as 43 cm. possessed advanced ovaries which also had residual ova from a previous spawning. If their growth rate in this area is similar to that of the species in Hawaii (Brock, 1954), which is not entirely unreasonable since skipjack in both areas seem to reach adulthood at about the same length, then these small fish must have spawned no more than 3 or 4 months previously. Earlier than that they would not have been large enough to be sexually mature. These observations, although not conclusive, indicate the possibility of multiple spawning within a season for individual skipjack.

FECUNDITY

Four skipjack with fork lengths of 43 to 74 cm. and with advanced ovaries were selected for fecundity determinations. Small sections were obtained from each of the ovaries and weighed to the nearest thousandth of a gram. The number of ova in the most advanced group in the sample was determined and multiplied by the ratio of ovary weight to sample weight to get an estimate of the total number of mature ova in the ovary. The results are presented in table 1, which also includes results obtained by Yabe (1954) for skipjack in Japanese waters. Estimates of the number of ova extruded at one spawning ranged from 0.1 million to 2 million, with an indication that the number spawned is related to the size of the skipjack, the larger fish spawning more ova. Joseph (1963) made fecundity determinations for 42 skipjack taken from the eastern Pacific Ocean. His estimates ranged from about 0.2 million to 1.5 million ova per spawning for skipjack with total lengths from 61.4 to 71.5 cm. Within the limits of his data, the size of the skipjack and the number of ova per spawning seemed to be related. Among some of the other tuna, a relation between the number of ova spawned and size of fish was found for the bigeye in the Pacific (Yuen, 1955) and Hawaiian yellowfin (June, 1953).

TABLE 1.—*Results of skipjack fecundity determinations*

Fish length	Ovary weight	Weight of sample	Advanced ova in sample	Estimated advanced ova in ovary (millions)
Centimeter	*Gram*	*Gram*	*Number*	*Number*
43.0	35	0.046	195	0.1
46.8 [1]				.1
50.5	112	.089	330	.4
56.2 [1]				.6
67.9	202	.080	352	.9
75.0	303	.029	192	2.0

[1] Data from Yabe (1954).

GONAD INDEX

Several investigators have discussed the possibility of using the relative ovary weight (ovary weight$\times 10^3$/fish weight) as a measure of maturity of tuna; e.g., June (1953), Yuen (1955), and Otsu and Uchida (1959). Schaefer and Orange (1956) also used the relative ovary weight to measure the maturity of skipjack, the only difference being that they used the cube of fish length instead of fish weight and a factor of 10^8 instead of 10^3. They called this relation the "gonad index," which is defined as $G.I.=\frac{w}{L^3}\times 10^8$, where "*G.I.*" is the gonad index, "*w*" the weight of the ovaries in grams, and "*L*" the fish length in millimeters. Schaefer and Orange plotted the gonad index against the 95th centile of the total ova-size frequency distribution and found a linear relation, the gonad index increasing with ova size, at least in their Area II of the eastern Pacific.

I calculated the gonad index for all the skipjack in my collection. Because only a sample of the most developed group of ova was measured, their

mean sizes were plotted against the gonad index in lieu of the 95th centile of the total ova-size frequency distribution. This difference should not affect greatly the comparison of my results with those of Schaefer and Orange.

Figure 5 is a scatter diagram showing my results, with the regression line obtained by Schaefer and Orange for their Area II data superimposed. Schaefer and Orange concluded that the gonad index was a reasonably reliable measurement of the degree of ova development; however, the largest gonad index they found was about 36, as compared to my 96. My data fit Schaefer and Orange's regression line fairly well up to a gonad index of 36. Above this value the relation seems to break down. There is a big overlap in gonad index between developing and advanced ovaries; therefore, it was not possible to make any inferences about the stages of development of skipjack in this area from the gonad index.

STAGE OF SEXUAL DEVELOPMENT AND SCHOOLING BEHAVIOR

As mentioned earlier, the sampling of skipjack by pole-and-line fishing was such that each sample represented fish captured from a single school. This circumstance made it possible to examine the within-school distribution of developmental stages.

A gross examination of the data (table 2) indicates that skipjack in the different stages of development were not distributed randomly within schools. Although fish in all stages of sexual development were found simultaneously in certain months, there was no instance in which all three stages of development were found within a school. Most of the schools were represented by skipjack in a single stage of development. A contingency test of homogeneity (Hoel, 1954, pp. 172–175) was applied to the data, testing the hypothesis that, with respect to stage of sexual development, skipjack are distributed randomly within schools. The probability ($X^2=510$, $df=144$) of obtaining the observed distributions by chance alone was less than 1 in 100. I conclude that there was indeed a relation between schools and stage of sexual development. The fact that fish of similar stages of sexual development tended to occur together, as well as the fact that those in several stages of development were found in a number of months, should be considered in the design of any study of spawning. Obviously, examination of a large number from only a few schools could lead to erroneous conclusions.

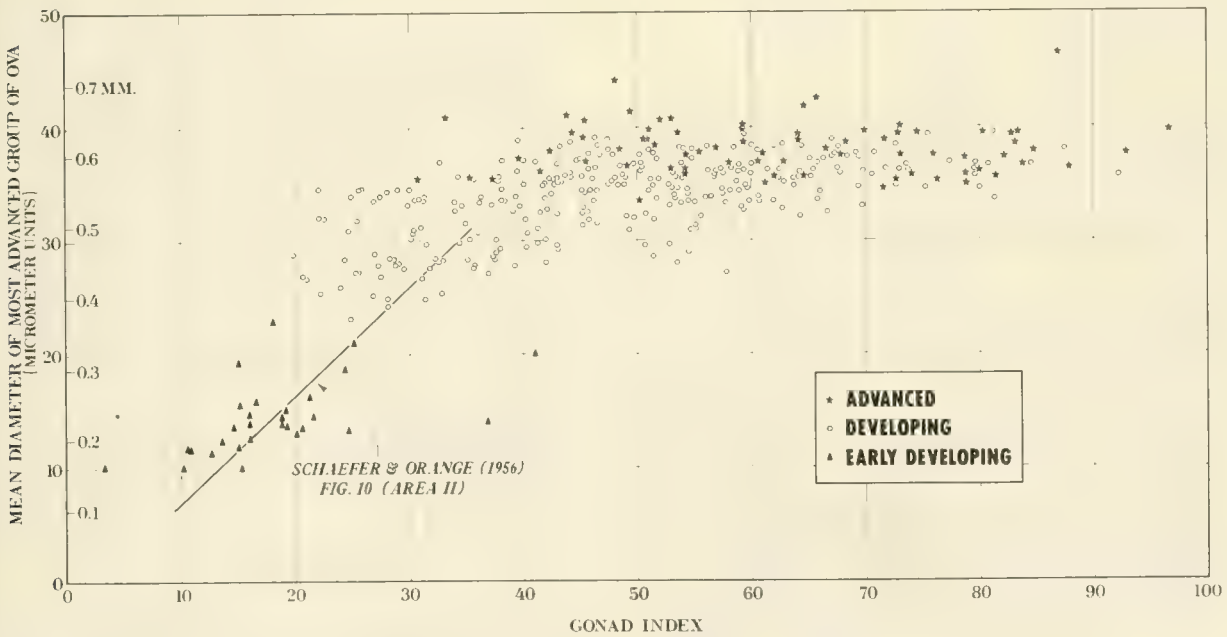

FIGURE 5.—Gonad index and mean diameter of largest group of ova.

TABLE 2.—*Numbers of skipjack in each stage of development in samples from single schools*

School	Stage of sexual development			Total
	Early developing	Developing	Advanced	
1	0	5	0	5
2	0	5	0	5
3	0	5	0	5
4	0	4	1	5
5	0	5	0	5
6	0	5	0	5
7	0	5	0	5
8	0	5	0	5
9	0	5	0	5
10	1	4	0	5
11	0	5	0	5
12	0	4	1	5
13	0	0	5	5
14	0	5	0	5
15	0	3	2	5
16	0	5	0	5
17	0	5	0	5
18	0	5	0	5
19	0	5	0	5
20	0	2	3	5
21	0	2	3	5
22	0	2	3	5
23	0	1	4	5
24	0	2	3	5
25	0	5	0	5
26	0	5	0	5
27	0	5	0	5
28	1	4	0	5
29	0	0	5	5
30	0	4	1	5
31	0	3	2	5
32	0	5	0	5
33	0	0	5	5
34	0	0	5	5
35	0	0	5	5
36	0	2	3	5
37	0	3	2	5
38	0	5	0	5
39	3	2	0	5
40	0	5	0	5
41	0	5	0	5
42	0	0	5	5
43	0	5	0	5
44	0	2	3	5
45	0	5	0	5
46	0	5	0	5
47	1	4	0	5
48	0	4	1	5
49	0	5	0	5
50	0	5	0	5
51	0	4	1	5
52	0	5	0	5
53	0	5	0	5
54	0	5	0	5
55	0	5	0	5
56	0	5	0	5
57	0	5	0	5
58	0	5	0	5
59	0	4	1	5
60	0	5	0	5
61	0	4	1	5
62	4	1	0	5
63	1	4	0	5
64	5	0	0	5
65	0	5	0	5
66	0	5	0	5
67	0	5	0	5
68	1	4	0	5
69	5	0	0	5
70	2	3	0	5
71	5	0	0	5
72	0	5	0	5
73	0	5	0	5
Total	29	271	65	365

As far as could be determined, there is very little in the literature regarding skipjack sexual development and schooling behavior. What are the causes of their apparent segregation by stage of sexual development? One possibility may be that skipjack about to spawn seek one another out, resulting in schools of similarly developed individuals. This explanation appears reasonable, for such a situation is probably more efficient for spawning purposes than a random distribution of spawning and nonspawning fish. Another explanation is that skipjack schools are relatively stable aggregations, with individuals in the group responding similarly to the environment and, therefore, developing similarly. However, on the basis of his size analysis of skipjack schools in Hawaii, Brock (1954) concluded that their composition is not stable. The pattern of tagged fish returns in Hawaiian waters seems to substantiate Brock's conclusion (Yamashita[2]). There probably is no simple explanation for this phenomenon. Undoubtedly there are many factors that influence the schooling behavior of skipjack, and the observed similarity of sexual development of the fish in the schools is probably a manifestation of a complex of factors.

SUMMARY

1. This study is based on the microscopic examination of ova from 402 pairs of ovaries collected from skipjack caught on exploratory fishing cruises from August 1956 through June 1958 around the Marquesas Islands and Tuamotu Archipelago.

2. The ova, ovaries, and skipjack were classified as being in the "early developing," "developing," "advanced," and "ripe" stages of development according to the physical characteristics of the most developed group of ova. Early developing ova ranged in appearance from simple transparent cells to cells with a well-developed nucleus; developing ova were opaque because of the deposition of yolk; advanced ova were opaque or semiopaque and contained a cluster of oil droplets or a single well-developed oil globule; ripe ova were almost perfectly spherical and transparent and contained a distinct straw-colored oil globule.

3. Skipjack in the Marquesas and Tuamotu areas are capable of first spawning when they are about 43 cm. long.

4. Scattered spawning may occur throughout the year, judging from the occurrence of developing skipjack in all months of sampling. The major spawning season, however, appears to be from November through April.

[2] Yamashita, Daniel T. Ms. Results of Hawaiian skipjack tagging. In files of the Bureau of Commercial Fisheries Biological Laboratory, Honolulu. (Manuscript.)

5. Although no conclusive statements can be made about the frequency of spawning of individual skipjack, the data indicate a possibility of more than one spawning per season.

6. Estimates of fecundity of skipjack ranged from 0.1 to 2 million ova per spawning.

7. It was not possible to make any inferences about the stage of development from the gonad index of skipjack.

8. A contingency test of homogeneity showed that there was a relation between skipjack schools and stage of sexual development; i.e., there was a tendency for skipjack in similar stages of sexual development to be found together in schools.

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FOOD OF YOUNG-OF-THE-YEAR WALLEYES IN LAKE ERIE

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ABSTRACT

Stomach contents were examined for 794 young-of-the-year (O-group) walleyes (*Stizostedion vitreum vitreum*) captured by trawls at 17 locations in western Lake Erie in June-November 1962. Food organisms were found in 92.5 percent of the stomachs. Food varied with geographic location and season of capture, but within areas and seasons, selection for certain species and sizes of prey was strong. Walleyes from the extreme western end of Lake Erie fed primarily on gizzard shad and alewives during the summer and shifted to emerald shiners during the fall. The stomach contents of walleyes from the Island region changed from mainly yellow perch during the summer to emerald shiners by the end of the year. Walleyes collected east of the Islands had consumed only smelt and yellow perch. The numbers of forage species caught with walleyes in trawls showed little correlation with the representation of these species in walleye stomachs. Walleyes fed on the smallest individuals of each species regardless of species preferences.

Among the fishes of primary economic importance in Lake Erie, the cisco or lake herring (*Coregonus artedi*), the whitefish (*C. clupeaformis*), the sauger (*Stizostedion canadense*), and the blue pike (*S. vitreum glaucum*) have become commercially unimportant, mostly in recent years. The last remaining "high-priced" fish left to the industry—the walleye (*S. vitreum vitreum*)—has also declined to a remnant population which fluctuates widely in abundance. The commercial catch (United States and Canadian) of walleyes has declined from a peak of 15,405,000 pounds in 1956 to a low of 717,000 pounds in 1962. The decline has been accompanied by demands for management of the fishery to restore and maintain abundance. Recent studies of the life history of the walleye were begun in 1957 to provide information essential to management. This report on feeding of young-of-the-year (O-group) walleyes at various seasons of the year and at different locations in western Lake Erie is a contribution to these studies.

Note.—Approved for publication Oct. 14, 1964.
This research was completed at the Biological Field Station, Sandusky, Ohio.

MATERIALS AND METHODS

The contents were examined of 794 stomachs from O-group walleyes of the 1962 year class collected in western Lake Erie at 17 locations in June–November 1962 (fig. 1). All collections were from U.S. waters and were made during routine trawling to ascertain the relative success of the hatching and survival of commercial and other species. The fish were caught in semi-balloon bottom trawls by Bureau of Commercial Fisheries vessels, *Musky II* (523 fish), *Kaho* (35), and an outboard-motor boat (233), and the Ohio Division of Wildlife vessel *Explorer* (3). The walleyes were preserved whole in 20 percent formalin after their abdomens had been slit; examinations and measurements were made in the laboratory. Food organisms were identified to the lowest taxonomic level possible. Stomach contents

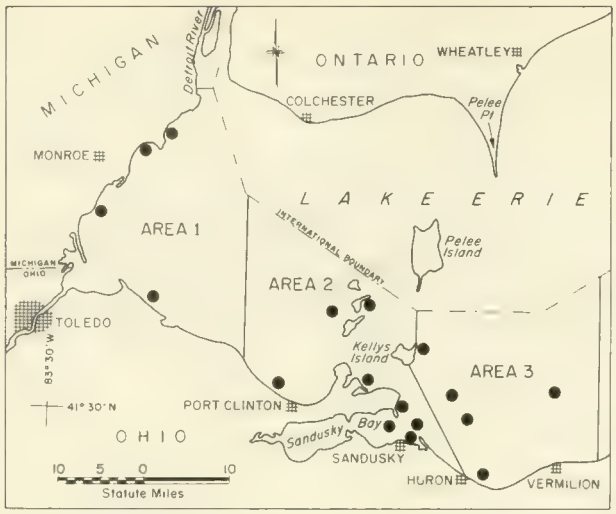

FIGURE 1.—Map of western Lake Erie showing locations where young-of-the-year walleyes were collected and areas by which data were analyzed. Dots represent collection locations.

were measured volumetrically by water displacement in a cylinder graduated to 0.1 ml. Items with a volume less than 0.1 ml. were listed as "trace". The entire stomach contents of 176 walleyes (41–74 mm. long) caught in June were examined with a dissecting microscope. No volumetric measurements were made of the food of these fish.

Counts were made of the O-group fish of the following species that were caught in the trawl hauls with the walleyes: Gizzard shad (*Dorosoma cepedianum*), alewife (*Alosa pseudoharengus*), American smelt (*Osmerus mordax*), emerald shiner (*Notropis atherinoides*), spottail shiner (*N. hudsonius*), trout-perch (*Percopsis omiscomaycus*), white bass (*Roccus chrysops*), yellow perch (*Perca flavescens*), and sheepshead or freshwater drum (*Aplodinotus grunniens*).

Data on food are presented separately for each of three areas in which walleyes were collected (fig. 1). Although the boundaries are somewhat arbitrary, each area differs ecologically from the others and each has its own characteristic fish fauna.

FOOD OF YOUNG WALLEYES IN DIFFERENT AREAS

The food of young-of-the-year walleyes in Lake Erie varied with geographic location and season of capture, but, within an area and season, selection for certain species and sizes of prey was strong. In general, little correlation existed between the numbers of various forage species present in the same catches with walleyes and the representation of these species in walleye stomachs.

Extreme Western Lake Erie (Area 1)

Food organisms were found in 94.7 percent of the 189 walleye stomachs (table 1). Gizzard shad and alewives were the principal food in July. Together they made up 72.7 percent of the total volume; gizzard shad occurred in 30.6 percent and alewives in 20.7 percent of the stomachs containing food. These species represented only 4.1 per-

TABLE 1.—*Food of young-of-the-year walleyes in extreme western Lake Erie in July, August, and October, 1962*

[Expressed in percentage of total volume (PV) and percentage frequency of occurrence (PO). Percentage frequencies based on numbers of stomachs containing food]

Food item	Dates of capture					
	July 17–24		August 14–16		October 15–18*	
	PV	PO	PV	PO	PV	PO
Insects:						
Tendipes pupae	<0.1	0.1	<0.1	13.9		
Tendipes larvae	...	...	<.1	2.8		
Fish:						
Alewife	32.7	20.7	16.7	8.3		
Emerald shiner			47.0	47.2	99.7	100.0
Gizzard shad	40.0	30.6	23.7	13.9		
Smelt	1.6	.9	...			
Spottail shiner	.3	.9				
Yellow perch	10.0	9.0	6.7	5.2		
Unidentifiable remains	15.4	53.2	5.9	33.3	.3	7.1
Number of stomachs	120		37		32	
Number of stomachs empty	9		1		4	
Average total length (mm.)	108		157		226	

TABLE 2.—*Young-of-the-year fishes taken in the same trawl hauls as walleyes (1962)*

[Expressed as percentage of total trawl catches in each indicated period [1]; no data for Area 3 because walleyes east of the Islands were taken in large-mesh trawls]

Dates of capture	Yellow perch	Emerald shiner	Gizzard shad	Alewife	Spottail shiner	White bass	Sheepshead	Trout-perch	Smelt
	Extreme western Lake Erie (Area 1)								
July 17–24	39.2		1.2	2.9	13.0	43.4	0.1		0.2
Aug. 14–16	16.9	0.4	5.4	5.5	9.3	58.5	3.6	0.3	.1
Oct. 15–18	66.3	12.4	<.1	4.2	14.7	.9	.2	.6	.7
	Island region (Area 2)								
June 25–27	97.1					2.5		0.2	0.2
July 2–18	99.0		0.7	<0.1	0.1	.2			
July 25–Aug. 1	38.8		11.9	.8	30.8	16.6	1.1		< 1
Aug. 20–30	79.6		1.2	.8	12.7	4.1	<.1	.4	1.2
Sept. 18–19	17.9	4.1	7.4	1.4	47.2	13.6	5.9	1.0	1.5
Oct. 29–Nov. 1	73.0	2.2	.1	.6	19.3	.4	1.9	1.9	.6

[1] Numbers of young-of-the-year walleyes caught are given in table 1 and table 4.

cent of the total number of fish taken in the trawl (table 2). In contrast, white bass made up 43.4 percent of the total number of O-group fish in the trawl catches from which the walleyes were obtained but none were found in walleye stomachs. Yellow perch composed 39.2 percent of the trawl catches but were in only 9.0 percent of the stomachs. The consumption of smelt and spottail shiners was negligible. No emerald shiners had been eaten.

Gizzard shad and alewives were being supplanted by other prey in stomachs of walleyes captured August 14–16. The volume of the two species in stomachs had dropped to 40.4 percent and the frequency of occurrence was only 13.9 percent for the gizzard shad and 8.3 percent for the alewife. Emerald shiners had entered strongly into the diet; they made up 47.0 percent of the volume and occurred in 47.2 percent of the stomachs. Emerald shiners were scarce, nevertheless, in trawl catches (0.4 percent of the total catches). The number of gizzard shad and alewives combined had increased to 10.9 percent of all fish caught, even though they had decreased in importance as food for walleyes. White bass, still the most abundant forage species available, had not been eaten.

The shift in food from gizzard shad and alewives to emerald shiners was complete in October when the identifiable stomach contents of 32 walleyes contained only emerald shiners. Emerald shiners had increased to 12.4 percent of the total catch of trawls in mid-October. Young-of-the-year yellow perch, although now the most available forage fish (66.3 percent of the total trawl catches), had not been eaten. Walleyes apparently sought more emerald shiners as the gizzard shad and alewives grew to a size that made them unsuitable prey (table 3).

Insects were eaten most commonly in August when the percentage frequencies of occurrence of pupae and larvae of the midge *Tendipes* were 13.9 and 2.8 percent, respectively. *Tendipes*, however, constituted a negligible amount of the total volume

TABLE 3.—*Comparison of total lengths (mm.) of young-of-the-year fish caught in trawls in extreme western Lake Erie and those taken from walleye stomachs (1962)*

Species and item	July 17–24		Aug. 14–16		Oct. 15–18	
	Trawls	Stomachs	Trawls	Stomachs	Trawls	Stomachs
Alewife:						
Average length	48	42	89	56	117	
Range of length	33–69	36–47	64–102	52–60	76–147	
Number	256	8	91	3	141	0
Emerald shiner:						
Average length			51	49	69	55
Range of length			38–61	45–54	51–86	48–65
Number	0	0	100	4	339	42
Gizzard shad:						
Average length	56	46	102	55	157	
Range of length	48–76	35–50	79–130	49–64	135–193	
Number	13	5	40	4	141	0
Sheepshead:						
Average length			64		109	
Range of length			33–89		61–142	
Number	0	0	98	0	49	0
Smelt:						
Average length	45		53		69	
Range of length	43–46		51–58		53–94	
Number	2	0	6	0	41	0
Spottail shiner:						
Average length	43		51		74	
Range of length	20–69		38–64		58–91	
Number	311	0	130	0	166	0
White bass:						
Average length	36		69		104	
Range of length	20–84		43–86		69–157	
Number	308	0	97	0	44	0
Yellow perch:						
Average length	53	36	66	53	81	
Range of length	41–74	33–42	58–76	53	66–97	
Number	482	6	142	1	219	0

of food. No other insects were present in the stomachs of walleyes from this area.

Island Region (Area 2)

Of the 562 walleyes collected from Area 2 (table 4) the late June sample of 176 individuals (mean length 55 mm.) required special treatment. All stomach contents of these small fish were examined with a dissecting microscope. The major food at this time was unidentifiable fish fry (frequency of occurrence—65.5 percent). Many of the fry probaby were yellow perch but positive identification was impossible, because of their small size. *Leptodora kindtii* appeared in 16.5 percent of the stomachs. Consumption of *Diaptomus*, *Cyclops*, and *Daphnia* was limited as was also that of unidentifible midge larvae and pupae. Ewers (1933) found *Leptodora* the most common of the Entomostraca in the diet of young walleyes and blue pike in western Lake Erie. The stomachs of 23 walleyes caught in the latter part of July 1929, and examined by Boesel [1] contained 82.9 percent Entomostraca and 17.1 percent fish by volume.

The 61 walleyes captured July 2–18 had been feeding entirely on fish fry. Yellow perch comprised 92.3 percent of the total volume. Seemingly little other food was available to small walleyes in this area at this season. Trawl catches in which the walleyes were taken consisted of 99.0 percent O-group yellow perch.

Young-of-the-year walleyes in other lakes of the Midwest consume large quantities of yellow perch. Eschmeyer (1950) found yellow perch in 42.1 percent of the stomachs of O-group walleyes of Gogebic Lake, Mich., during June 24 to July 10, 1941. Yellow perch also made up 68 percent of the total volume of food. Yellow perch constituted 77 percent by volume of the stomach contents of O-group walleyes in Mille Lacs Lake, Minn., in June–September (Maloney and Johnson, 1957).

The 219 walleyes taken July 25 to August 7 had eaten a diversity of organisms. Yellow perch continued to be the major food (total volume—64.3 percent; frequency of occurrence—72.3 percent). They were also the most available prey

[1] Boesel, M. W. 1929. A preliminary report on the food of certain insect feeding fishes of Lake Erie. MS., Department of Zoology, Ohio State University, 30 pp.

TABLE 4.—*Food of young-of-the-year walleyes in the Island region in June–November 1962*

[Expressed in percentage of total volume (PV) and percentage frequency of occurrence (PO). Percentage frequencies based on numbers of stomachs containing food]

Food item	Dates of capture									
	June 25–27	July 2–18		July 25–Aug. 7		Aug. 20–30		Sept. 18–19		Oct. 29–Nov. 1	
	PO [1]	PV	PO	PV	PO	PV	PO	PV	PO	PV	PO
Algae	0.5										
Copepods:											
Diaptomus oregonensis	.5										
Diaptomus spp	.5										
Cyclops vernalis	1.9										
Cyclops spp	2.9										
Cladocerans:											
Daphnia retrocurva	1.9										
Daphnia galeata	.5										
Daphnia spp	1.5										
Leptodora kindtii	16.5										
Unidentifiable remains	.5										
Insects:											
Tendipes pupae				<0.1	7.0	<0.1	1.8				
Tendipes larvae				<.1	.5						
Unidentified midge pupae	2.4										
Unidentified midge larvae	3.4										
Ichneumonidae				<.1	.5						
Fish:											
Alewife				12.1	6.1						
Emerald shiner				4.5	3.3	3.0	3.5	9.3	22.9	93.0	88.8
Gizzard shad				12.1	4.2	.8	1.8	28.0	17.1		
Percina spp				.1	.5						
Smelt				.6	.9			1.5	8.6		
Spottail shiner				1.5	1.4						
Yellow perch	1.5	92.3	58.6	64.3	72.3	91.5	84.2	60.4	65.7	7.0	11.1
Unidentifiable fry	65.6	7.7	55.2								
Unidentifiable remains				4.8	31.0	4.7	19.3	.8	8.6	< 1	11.1
Number of stomachs	176	61		219		60		36		10	
Number of stomachs empty	27	3		6		3		1		1	
Average total length (mm.)	55	79		132		183		214		239	

[1] Volumes not measured in this collection.

(38.8 percent of all fish taken by trawl). Although gizzard shad and alewives made up 24.2 percent of the total volume of food, they were present in relatively few stomachs. Similarly, few spottail shiners had been eaten (frequency of occurrence—1.4 percent) even though they were readily available (30.8 percent of the trawl catches). Emerald shiners were not taken by the trawl but were in 3.3 percent of the stomachs. *Tendipes* pupae were more prominent at this time than in any other period (frequency of occurrence—7.1 percent). Maloney and Johnson (1957) reported that dipterous larvae occurred in the stomachs of walleyes taken in August in Lake Winnibigoshish, Minn.

Yellow perch made up the bulk of the food of the walleyes captured in the Island area, August 20–30 (total volume—91.5 percent; frequency of occurrence—84.2 percent). Gizzard shad had almost disappeared from the stomachs (total volume—0.8 percent). Again, emerald shiners had been eaten but were not in the trawl catches. Walleyes may have been seeking out this minnow. On the other hand, trawl catches may not provide an exact index of relative abundance of emerald shiners because this fish occasionally frequents the surface waters and hence becomes unavailable to bottom trawls.

The importance of yellow perch had begun to decline by September 18–19 (total volume—60.4 percent; frequency of occurrence—65.7 percent); perch were being supplanted by emerald shiners (total volume—9.3 percent; frequency of occurrence—22.9 percent). Trawl catches indicated that the availability of yellow perch had decreased while that of the emerald shiners had increased (table 2).

The few walleyes caught between October 29 and November 1 showed a further shift from yellow perch (total volume—7.0 percent; frequency of occurrence—11.1 percent) to emerald shiners (total volume—93.0 percent; frequency of occurrence—88.8 percent). Doan (1941) stated that emerald shiners constituted 82 percent of the volume of food eaten by 62 walleyes, 10–17 inches long, caught at Put-In-Bay, Ohio, in November and December 1940.

Evidence from extreme western Lake Erie (Area 1) suggests that the walleye prefers gizzard shad or alewives during its early months of life, even though ample numbers of young yellow perch (and other species) of suitable size are available. It is apparent from the fish taken in the Islands region (Area 2), however, that where yellow perch almost completely dominate the food supply, the walleye can and does feed heavily upon them. The shift to emerald shiners that occurred in the late summer and autumn in both Areas 1 and 2 may be traceable to different causes. In Area 1, the emerald shiners became prominent in the food of walleyes when the gizzard shad and alewives became too large to eat. In Area 2, the change probably reflects species rather than size preference since both the emerald shiners and the yellow perch captured in October were about the same size (table 5).

East of the Island Region (Area 3)

Forty-three O-group walleyes were collected off Huron and Vermilion, Ohio, and east of Kelleys Island in July, August, September, and October. The 38 fish that had food in their stomachs had eaten almost exclusively smelt and yellow perch (table 6). Yellow perch were the only food of walleyes in the small July collection. Some smelt were eaten in August, and by September this species had become the only food in almost all stomachs. No suitable records are available of the relative numbers of O-group fish living with the walleyes because most were taken in trawls with large-mesh cod ends that permitted the escape of most small fish. A cursory examination of the catches did reveal, however, that the bulk of forage available to the walleyes east of the Islands consisted of smelt and yellow perch in all seasons.

ACKNOWLEDGMENTS

The Bureau of Commercial Fisheries vessel *Kaho* and the Ohio Division of Wildlife vessel *Explorer* collected walleyes for stomach analysis. Jarl Hiltunen assisted in the identification of the immature midges, and LaRue Wells helped identify crustaceans. Vernon C. Applegate advised in the preparation of the manuscript.

TABLE 5.—*Comparison of total lengths (mm.) of young-of-the-year fish caught in trawls in the Island region and those taken from walleye stomachs (1962)*

Species and item	July 2–18		July 25–August 7		August 20–30		September 18–19		Oct. 29–Nov. 1	
	Trawls	Stomachs	Trawls	Stomachs	Trawls	Stomachs	Trawls	Stomachs	Trawls	Stomachs
Alewife:										
Average length	51	-	79	50			97			
Range of length	28–61		64–89	46–59			61–117			
Number	111	0	54	8	0	0	15	0	0	0
Emerald shiner:										
Average length				42		44		49	66	62
Range of length				37–45		44		43–55	56–76	55–65
Number	0	0	0	3	0	1	0	8	100	9
Gizzard shad:										
Average length			84	54			102	65		
Range of length			58–117	44–64			61–147	57–75		
Number	0	0	174	6	0	0	253	6	0	0
Sheepshead:										
Average length			69							
Range of length			30–99							
Number	0	0	193	0	0	0	0	0	0	0
Smelt:										
Average length				35	53			48		
Range of length				30–40	46–58			45–53		
Number	0	0	0	2	4	0	0	3	0	0
Spottail shiner:										
Average length	38		43	35	53		58		76	
Range of length	25–56		28–58	27–40	38–74		51–71		51–91	
Number	87	0	209	4	158	0	104	0	86	0
White bass:										
Average length	38		56		53		109		84	
Range of length	25–56		28–81		41–79		51–147		53–124	
Number	126	0	298	0	152	0	209	0	78	0
Yellow perch:										
Average length	41	25	48	37	58	49	71	51	71	50
Range of length	30–51	23–28	30–76	26–46	48–76	42–61	56–91	43–64	53–94	50
Number	121	6	573	79	171	48	75	45	186	1

TABLE 6.—*Food of young-of-the-year walleyes captured in Area 3 in July, August, September, and October, 1962*

[Expressed in percentage of total volume (PV) and percentage frequency of occurrence (PO). Percentage frequencies based on numbers of stomachs containing food]

Food item	Dates of capture							
	July 19		Aug. 23–30		Sept. 6–26		Oct. 10	
	PV	PO	PV	PO	PV	PO	PV	PO
Smelt			16.1	50.0	93.3	63.6	95.7	90.9
Yellow perch	100.0	100.0	83.9	100.0			4.3	4.5
Unidentifiable fish remains					.7	36.4	<.1	4.5
Number of stomachs	4		2		15		22	
Number of stomachs empty	1		0		4		0	
Average total length (mm.)	82		174		218		236	

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EFFECT OF THE SPAWNING BED ENVIRONMENT ON REPRODUCTION OF PINK AND CHUM SALMON [1]

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ABSTRACT

Mortality of 5 brood years of pink salmon, *Oncorhynchus gorbuscha*, and chum salmon, *O. keta*, in spawning beds of three Southeastern Alaska streams was studied. Eggs and larvae were sampled periodically, and mortality was associated with certain environmental factors: The supply of dissolved oxygen, the stability of spawning beds, and freezing.

Total mortality between spawning and fry emergence typically varied between 75 and 99 percent in the study areas. High mortality occurred during low and high stream discharge and freezing air temperatures. Mortalities ranging from 60 to 90 percent of deposited eggs occurred in association with low dissolved oxygen levels during and after the spawning period. Movement of gravel in certain instances was associated with the removal of 50 to 90 percent of eggs and larvae present in spawning beds. Freezing caused up to 65 percent mortality of eggs and larvae in one stream.

Low dissolved oxygen levels occurred once in 5 years. This occurrence was associated with unusually low water during spawning in late summer. Mortality during periods of heavy precipitation was highly variable. In one instance, a 90-percent mortality occurred where wood debris was deposited within the high water channel. Wood debris floating over spawning beds was not damaging to eggs and larvae. There were several instances where mortality estimated at almost 50 percent occurred with no evidence that deposited wood debris shifted position. High mortality from freezing occurred only in the stream having the lowest minimum discharge.

Pink salmon, *Oncorhynchus gorbuscha*, and chum salmon, *O. keta*, are the only species of Pacific salmon in North American streams using fresh water [2] solely for spawning. The young of these species, with minor exceptions, migrate to sea soon after emerging from spawning beds, while the young of chinook salmon, *O. tshawytscha;* sockeye, *O. nerka;* and coho, *O. kisutch*, may remain in fresh water for many months.

Adult pink and chum salmon commonly migrate into coastal streams to spawn in summer and early autumn. They excavate pockets in riffle areas and deposit and bury their eggs in the bottom. Surviving embryonic and larval salmon remain in the spawning bed for periods up to 8 months, and fry usually emerge and migrate seaward the spring after spawning.

The spawning bed protects eggs and larvae against predators, light, displacement, and mechanical injury. Despite this protection, mortality from time of egg deposition to fry emergence commonly exceeds 75 percent.

Estimates of total fresh-water mortality of pink and chum salmon have been published for McClinton, Morrison, Nile, and Hook Nose Creeks, British Columbia (Pritchard, 1948; Neave, 1953;

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[2] Includes intertidal areas periodically inundated by salt water or brackish water.

Hunter, 1959); and Sashin Creek, Southeastern Alaska (Merrell, 1962). For the brood years studied, total mortality in these streams ranged from 76 to 99.9 percent. Although these estimates fail to differentiate among mortalities occurring during (1) adult migration, (2) egg and larval development, and (3) fry migration, other evidence indicates that the largest portion of total fresh-water mortality occurs between the time eggs are deposited and fry emerge.

Typical results are seen in mortality studies at Hook Nose Creek (Hunter, 1959). Although Hunter found that total deaths varied considerably from year to year, losses before spawning appeared to be consistently small. The number of fry consumed by predators was fairly constant from year to year and was usually a small fraction of the potential egg deposition. Most deaths occurred between spawning and fry emergence. Hunter's data showed that over a 10-year period, 69–94 percent of the eggs potentially available for deposition were lost before emergence of fry.

Increased utilization of streams and watersheds by logging, mining, and other multiple-use activities has caused concern about the welfare of salmon. A thorough understanding of the factors causing mortality in spawning beds will be required to evaluate the effects of multiple-use activities on pink and chum salmon.

In 1956 the Bureau of Commercial Fisheries gave Saltonstall-Kennedy Act funds to the Fisheries Research Institute (FRI), University of Washington, to study the effects of logging on pink salmon streams in Alaska. These studies concentrated on identifying the time and magnitude of mortality and determining the factors responsible. This paper reviews past work on factors causing mortality in spawning beds and reports findings of field studies in three Southeastern Alaska spawning streams. Field observations on mortality and associated environmental factors thought to cause mortality are described.

REVIEW OF ENVIRONMENTAL REQUIREMENTS OF EGGS AND LARVAE

Given an environment free of mechanical disturbances, the growth, development, and survival of salmon eggs and larvae depend largely upon physical and chemical characteristics of the surrounding water. Properties of water that affect eggs and larvae include temperature, dissolved oxygen content, velocity, mineral and waste metabolite content, and osmotic pressure.

The spawning bed environment is greatly influenced by weather and characteristics of the streambed, stream, and watershed. The quality of intragravel water [3] is influenced in part by the hydrological regimen. Environmental changes within spawning beds can accompany changes in tide level, precipitation, and air temperature. Periods of spawning and development very likely coincide with the seasonal conditions that offer maximum opportunity for survival of the young salmon.

SOURCES OF INTRAGRAVEL WATER

To survive, eggs and larvae must receive an ample supply of oxygenated water suitable in temperature and free of toxic substances. The source of intragravel water may govern to a large extent its physical properties and its suitability for eggs and larvae.

Ground water and surface stream water are the two primary sources of intragravel water. In spawning beds of pink and chum salmon, surface stream water is the primary source of intragravel water (Sheridan, 1962a), while in spring-fed spawning beds commonly used by other salmonid species; e.g., sockeye salmon, ground water may be an important source of intragravel water.

Vaux (1961, 1962) showed that interchange between stream and intragravel water occurred when certain hydraulic requirements of the stream and streambed were satisfied. He formulated models which showed the direction of interchange depends on the curvature of the gravel surface profile. Where the profile was concave, water upwelled; where it was convex, a downdraft occurred. In the absence of curvature, there was no interchange, provided permeability and gravel bed depth did not vary. Vaux verified these relations with field and laboratory experiments. Figure 1 illustrates the direction of interchange with change in curvature of the stream bottom.

WATER TEMPERATURE

Water temperature controls the rate of growth and the developmental and metabolic processes of the salmon embryo. It also affects other water quality characteristics, such as dissolved oxygen concentration.

[3] The term "intragravel water" refers to water occupying interstitial spaces within the streambed.

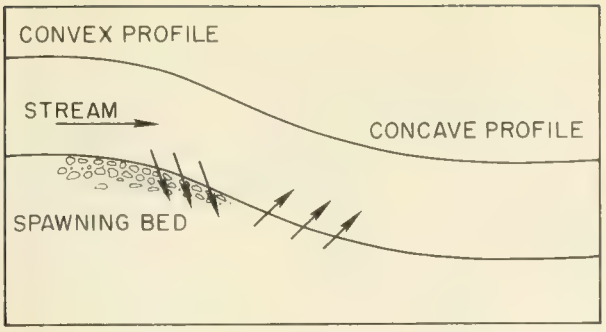

FIGURE 1.—Changes in direction of interchange with changes in curvature of the stream bottom (from Vaux, 1962). Arrows indicate direction of interchange.

The temperature of intragravel water in pink salmon spawning beds is controlled largely by stream water temperature. Sheridan (1961) obtained a linear correlation coefficient of 0.99 when he related intragravel and stream water temperatures.

Pink and chum salmon embryos and larvae survive in streams where water temperatures drop to 0° C. James (1956) reported water temperatures slightly below 0° C. in pink and chum salmon spawning streams. In an experiment with pink salmon embryos, Combs and Burrows (1957) varied water temperature to coincide with variations observed in Sashin Creek, Southeastern Alaska. They found that embryos reared at 5.5° C. for 30 days and then at 0.5° C. to hatching had almost no mortality.

Information is lacking on tolerance of pink and chum salmon eggs and larvae to high temperature, but studies with other salmonid species suggest that temperatures of 15° C. or higher may be tolerated. Chinook salmon embryos exposed to 20° C. water died at all developmental stages, while embryos exposed to 17° C. water died only at hatching (Donaldson, 1955). Larvae of Atlantic salmon, *Salmo salar*, and brown trout, *S. trutta*, survived 16 days in 20° C. water (Bishai, 1960).

Pink and chum salmon normally spawn on declining water temperature after maximum summer temperatures. Sheridan (1962b) reported that pink salmon typically spawned in Southeastern Alaska streams after water temperatures declined to 10° C. or less in late summer. Mean water temperature in Hook Nose Creek was reported to be 12° C. or less when pink and chum salmon spawned (Hunter, 1959). It would appear, therefore, that high temperature seldom exerts a direct lethal stress on pink and chum salmon eggs and larvae.

DISSOLVED OXYGEN SUPPLY

Oxygen is transported to the embryo by diffusion. After water hardening, the capsule of a newly fertilized egg is permeable to oxygen molecules but impermeable to water molecules (Krogh and Ussing, 1937).

The oxygen consumption rate per unit mass of embryonic tissue appears fairly constant over most of the developmental period. During the last two-thirds of the period, the oxygen consumption per gram of embryo remained almost constant for Atlantic salmon (Hays, Wilmot, and Livingstone, 1951). The rate of oxygen consumption for chum salmon was highest but variable during the first one-third of the developmental period and fairly constant thereafter (Alderdice, Wickett, and Brett, 1958).

The rate at which oxygen is consumed by salmon embryos decreases with decreasing dissolved oxygen content of the water below a certain "limiting level" while at dissolved oxygen levels higher than the limiting level, the rate is independent of pressure or content of dissolved oxygen. The limiting level corresponds to the dissolved oxygen content or partial pressure below which normal metabolic functions are affected. There is evidence, also, that the limiting level may vary in a complex manner with temperature and stage of development (Lindroth, 1942; Hays, Wilmot, and Livingstone, 1951).

Alderdice, Wickett, and Brett (1958) calculated theoretical values of the limiting dissolved oxygen level for chum salmon embryos by using an equation originated by Harvey (1928) and later modified by Krogh (1941). The equation is

$$C_0 = \frac{SRT}{3U} \qquad (1)$$

where C_0=limiting level of oxygen dissolved in the external medium in atmospheres

R=radius of the egg in cm.

S=ml. of oxygen consumed/g. of embryo/minute.

T=thickness of the capsule in cm.

U=diffusion coefficient of oxygen through the capsule in ml. O_2/cm.^{2} of surface/cm. of thickness/minute.

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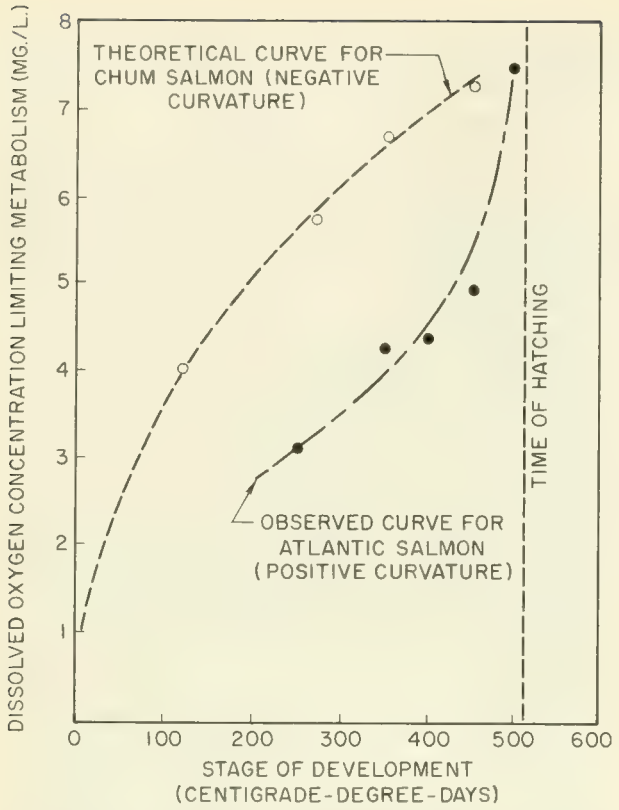

FIGURE 2.—Concentration of dissolved oxygen first reducing rate of oxygen consumption by salmon embryos. Upper curve is from Alderdice et al. (1958). Lower curve is from Hays et al. (1951). Water temperature is taken to be 10° C., and a centigrade-degree-day is equivalent to a constant temperature of 1° C. above 0° C. over a 24-hour period.

In figure 2, the theoretical values of C_0 at 10° C. obtained for chum salmon by Alderdice et al. (1958) (upper curve) are compared with limiting levels determined experimentally for Atlantic salmon by Hays et al. (1951). The most striking difference between theoretical and observed limiting dissolved oxygen concentrations is the sign of curvature of the connected points. It is doubtful if difference in species would account for positive curvature in Atlantic salmon and negative curvature in chum salmon. The validity of equation (1) as it applies to salmonid embryos is, therefore, questioned.

Wickett (1954) pointed out that the delivery rate of oxygen to an egg or a larva is a function of water velocity as well as oxygen content. Others (Coble, 1961; Shumway, 1960; Silver, 1960; Silver, Warren, and Doudoroff, 1963) gave experimental evidence that variations in velocity affected embryonic growth, development, and survival in much the same manner as variations in oxygen content.

According to curves of figure 2, embryos are most susceptible to low dissolved oxygen levels near the time of hatching. Evidence of this was presented by Hays and Armstrong (1942) and Garside (1959), who observed high mortality at hatching. Because mortality increased with slight increases in temperature, these authors attributed death to an inadequate amount of dissolved oxygen diffusing through the egg capsule.

The effect of oxygen supply rate on growth, development, and survival of salmonid embryos has been investigated by several workers. The dissolved oxygen level causing 50-percent mortality of chum salmon embryos increased from about 0.4 mg./1. at fertilization to 1.4 mg./1. at hatching, when apparent velocity [4] and temperature were maintained at 85 cm./hour and 10° C. (Alderdice et al., 1958). Coho salmon eggs incubated at near true velocity of 3 cm./hour, a temperature of 9° C., and an oxygen level of 2.4 mg./1. survived to hatch but produced larvae about one-third the volume of controls (Shumway, 1960). Similar findings were reported by Silver, Warren, and Doudoroff (1963), who experimented with chinook salmon and rainbow trout, *Salmo gairdneri*, embryos. At near true velocity of 6 cm./hour and a dissolved oxygen content of 2.6 mg./1., Silver (1960) observed abnormal development. At similar low levels of dissolved oxygen, Alderdice et al. (1958) and Garside (1959) described abnormal development of caudal regions during somite formation. Garside also found that the development rate was retarded significantly by reduced oxygen level.

Larvae are more tolerant of low dissolved oxygen levels than are embryos. For Atlantic salmon, Hays et al. (1951) found the dissolved oxygen concentration limiting metabolism of embryos to be 7.5 mg./1. at 10° C. After the eggs hatched the limiting concentration decreased to 4.5 mg./1. Initiation of active respiration across gill membranes having vastly increased respiratory areas may have caused the sudden decrease in limiting oxygen concentration.

[4] Apparent velocity is measured by dividing the rate of flow by the cross-sectional area of the bed through which the water had passed. The actual or true velocity is greater than the apparent velocity where part of the cross-sectional area is occupied by eggs or other objects.

Several general conclusions may be drawn regarding the dissolved oxygen requirements of pink and chum salmon embryos and larvae. First, the supply of dissolved oxygen made available to an embryo or larva is both a function of dissolved oxygen content and flow velocity of intragravel water. Second, the rate of oxygen consumption per unit mass of embryonic tissue is little affected by growth over most of the developmental period up to hatching. Hence, the rate of oxygen consumption by a population of embryos is possibly a simple function of the biomass present. Third, oxygen levels limiting metabolic processes and causing mortality approach a maximum shortly before hatching. After hatching, there is a sharp decline in limiting levels of dissolved oxygen. By considering only the requirements of eggs and larvae and neglecting changes in the environment, it would appear that the dissolved oxygen requirements of eggs become most critical at hatching.

METABOLIC WASTE PRODUCTS

Two metabolic waste products excreted by salmon eggs and larvae are free carbon dioxide and ammonia. Both are toxic to aquatic organisms.

The effect of free carbon dioxide on the physiology of blood has been studied exhaustively. Jacobs (1920) showed that molecules of free carbon dioxide passed readily through living cell membranes. The ability of eggs and larvae to respire is influenced by the blood's affinity for oxygen, and there is a loss of affinity for oxygen in the presence of free carbon dioxide (Bohr effect). Salmonid blood in vitro lost half of its oxygen-combining capacity in the presence of 150 mg./l. of free carbon dioxide at 15° C. (Irving, Black, and Safford, 1941). Since the oxygen tension equal to one-half saturation is considered to be the minimum compatible with exchange of oxygen to the tissues, a salmonid having its blood oxygen-combining capacity reduced 50 percent would die theoretically of suffocation.

Only a few investigators have investigated the effect of free carbon dioxide on salmonid eggs and larvae. Bishai (1962) induced a marked metabolic stress on Atlantic salmon and brown trout larvae by subjecting them to high free carbon dioxide levels. High mortality among trout embryos occurred at free carbon dioxide levels between 55 and 80 mg./l. in hatchery water (Surber, 1935). Increased mortality of chum salmon embryos was caused by 125 mg./l. of free carbon dioxide (Alderdice and Wickett, 1958). Additional information on the effect of high free carbon dioxide content in conjunction with low dissolved oxygen levels on growth, development, and survival of salmon eggs and larvae will be required before relationships observed between mortality and quality of intragravel water can be fully evaluated.

Ammonia is the most toxic metabolite. Ammonia excreted by salmon eggs and larvae is removed by the surrounding water, but it is possible that toxic concentrations of ammonia occur where the density of eggs and larvae is high and the circulation of intragravel water is poor.

The toxicity of ammonia is related directly to the concentration of free ammonia (NH_3) or non-ionized ammonium hydroxide ($NH_3 \cdot H_2O$) in solution. Ionization of $NH_3 \cdot H_2O$ occurs according to the equilibrium equation

$$NH_3 \cdot H_2O \rightleftarrows NH_4^+ + OH^-$$

Ionization is nearly complete at pH 7.0 and lower, and ammonia is least toxic in waters having high concentrations of hydrogen ions (pH <7.0). Formation of carbonic acid from respired free carbon dioxide would, therefore, tend to decrease the toxicity of ammonia.

Reviews of influence of ammonia on fish have been given by Doudoroff and Katz (1950) and Doudoroff (1957). These authors concluded that additions of 2 to 7 mg./l. of ammonia to natural waters could kill fish. Experiments by Wuhrmann and Woker (1948) showed that concentrations of only 1.2 mg./l. of NH_3 were lethal to fresh-water fish of the genus *Squalius*. They also found that 1.3 mg./l. of NH_3 killed rainbow trout fry.

According to Wolf (1957a, 1957b), blue-sac disease was induced by subjecting salmonid embryos to high concentrations of ammonia. The incidence of disease was roughly proportional to the contact period and the NH_3 concentration.

SALINITY

Pink and chum salmon spawn in intertidal areas of streams, and in some streams more fry are

produced in intertidal areas than in upstream areas (Kirkwood, 1962). From field observation alone, it is apparent that pink and chum salmon eggs and larvae can tolerate intermittent high salinity.

Rockwell (1956) exposed pink and chum salmon eggs and larvae to constant high salinity and found no evidence that fertilization of eggs was affected by salinities up to 18°/₀₀. The tolerance of embryos to sea water was a function of osmotic pressure, time of exposure, and stage of development. Mortality was attributed to dehydration. He found a marked reduction in the rate of early growth of chum salmon embryos at constant salinities of 12°/₀₀ and greater and a total mortality to hatching at a salinity of 12°/₀₀. At 6°/₀₀ salinity, survival to hatching was less than that in the controls.

Larvae are more tolerant of high salinity than eggs. According to Rockwell (1956), salinities as high as 18°/₀₀ killed few pink salmon larvae. Chum salmon larvae were less tolerant, some dying at a salinity of 12°/₀₀.

Salinity of intragravel water in pink and chum salmon intertidal spawning beds is influenced markedly by tidal action. Hanavan and Skud (1954) found salinity of intragravel water of pink salmon spawning beds corresponds closely to salinity of overlying water. Also, they observed high survival of pink salmon eggs and larvae where tidal inundation prevailed during 35 percent of the incubation period. Ahnell (1961) observed that the salinity of intragravel water remained high for a period after the tide had receded and after fresh water had flowed over the streambed. He found also that high salinity of intragravel water was frequently associated with low dissolved oxygen concentration.

The effect of salinity on pink and chum salmon fry production is still poorly understood, although highly productive spawning areas exist in intertidal zones of streams (Kirkwood, 1962). Eggs and larvae of both species can tolerate intermittent high salinity, but tolerance levels have not yet been defined. Also, the retention of salt water by spawning beds and the influence of salt water on temperature, oxygen levels, and water velocity have not been studied in detail. The ultimate need is to determine the relative potential of intertidal and upstream areas to produce fry.

PERMEABILITY OF BOTTOM MATERIALS

It has already been pointed out that the oxygen delivery rate to an egg or larva is a function of both the oxygen content and velocity of intragravel water. Apparent velocity of water flowing within the streambed can be described by the equation.

$$v = \eta i \qquad (2)$$

Where v = apparent velocity,
η = permeability coefficient, and
i = hydraulic gradient.

According to this equation, apparent velocity of intragravel water varies directly with the permeability of materials through which it passes. Other factors being equal, the permeability of bottom materials in spawning beds should be directly related to their potential to produce salmon fry; Wickett (1958) gave evidence that the average survival of pink and chum salmon eggs and larvae in four British Columbia streams was directly related to the permeability of bottom materials (fig. 3).

The permeability of bottom materials is a function of particle compaction, arrangement, and size. McNeil and Ahnell (1964) showed that the permeability of bottom materials in a pink salmon spawning bed is inversely related to the fraction of fine particles composing the total volume of the bed. Thus, the resistance to flow caused by the presence of fine particles in salmon spawning beds must govern, to a large extent, their potential to produce healthy fry.

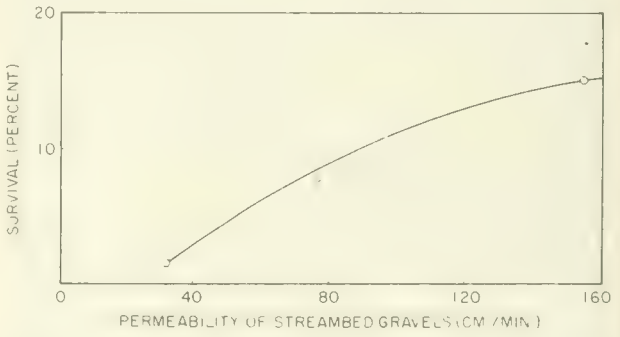

FIGURE 3.—Observed relation reported by Wickett (1958) between permeability and survival of pink and chum salmon to migrant fry.

STABILITY OF SPAWNING BEDS

Dislodgment of salmonid eggs and larvae from spawning beds during high water has been described by a number of workers (Hobbs, 1937; Hutchinson and Shuman, 1942; Davidson and Hutchinson, 1943; Withler, 1952; Needham and Jones, 1959; Wickett, 1959). Estimates of mortality rates from gravel movement have not been made in most instances. Furthermore, little is known about the interactions of factors creating unstable conditions in spawning beds and causing mortality rates to increase.

Changes in surface profile occur where a streambed degrades or aggrades. It is possible, however, for bed movement to occur without an associated change in surface profile or gradient (Mackin, 1948). One important unsolved problem is to determine if bed movement can cause appreciable mortality where there is no associated change in streambed gradient.

The effect of the pool-riffle complex on the capacity of streams to produce pink and chum salmon is not yet well understood. Factors important in generating the pool-riffle complex include debris in the high-flow channel (Bishop and Shapley, 1963) and bends in the channel. Shifts in position of debris create unstable conditions in the spawning bed which could lead to dislodgment of salmon eggs and larvae.

METHODS

STUDY STREAMS

Field studies described in this report were conducted mostly in three streams located in the Kasaan Bay region of Prince of Wales Island, Southeastern Alaska: Harris River, Indian Creek, and Twelvemile Creek (fig. 4). Watersheds of the study streams are precipitous. Soils are shallow and underlaid with impermeable materials. Except for muskegs, which are poorly drained areas, the watersheds have a very low capacity to retain water. Runoff is rapid, and peak discharges occur within a few hours after the beginning of heavy rainfall. These high discharges occur mostly in autumn.

The study streams occasionally freeze over in winter, when water temperatures near 0° C. have been recorded for as long as 6 consecutive days; summer water temperatures rarely exceed 13° C. (James, 1956).

Adult pink and chum salmon usually enter the study streams to spawn between mid-August and late September. Spawning occurs mostly in September. A large percentage of pink salmon spawn in intertidal areas, where the density of spawners is highest in most years.

Harris River is the largest of the three study streams. Salmon have access to about an 8-mile section of the main stream and its North Fork. Chum salmon were observed to spawn mostly in the North Fork, but pink salmon exhibited a marked preference for a ½-mile section of the upper intertidal zone. Discharge during the spawning period commonly fluctuates between 22 and 1,800 cubic feet per second (c.f.s.). During autumn storms, average daily discharge may approach 5,000 c.f.s. Width of intertidal spawning riffles during low flow averages about 60 feet. Spawning beds consist of materials mostly less than 4 inches in diameter.

Indian Creek is the smallest of the study streams but exhibits pronounced fluctuations in discharge. During the spawning period, discharge commonly varies between 4 and 300 c.f.s. Average daily discharge during autumn storms approaches 900 c.f.s. some years, and a peak instantaneous discharge of 6,400 c.f.s. was recorded on one occasion (McNeil, Shapley, and Bevan, 1962). Pink salmon spawn in Indian Creek, primarily in an intertidal section one-fourth mile long beginning at the confluence with Harris River. The average width of Indian Creek spawning beds at low flow is about 25 feet. Spawning beds consist of materials mostly less than 6 inches in diameter.

Twelvemile Creek has a more stable discharge than either Harris River or Indian Creek. During spawning, average daily discharge usually varies between 12 and 300 c.f.s. During autumn storms, average daily discharge rarely exceeds 600 c.f.s. Intertidal spawning areas average about 45 feet wide during low flow, and spawning beds consist mostly of materials less than 4 inches in diameter, and contain a high percentage of sand and silt. About 5 miles are believed accessible to salmon, but the distance has not been measured. Heaviest densities of spawning pink salmon have been observed in the intertidal zone. Chum salmon, less abundant here than pink salmon, commonly spawn in the intertidal zone, too.

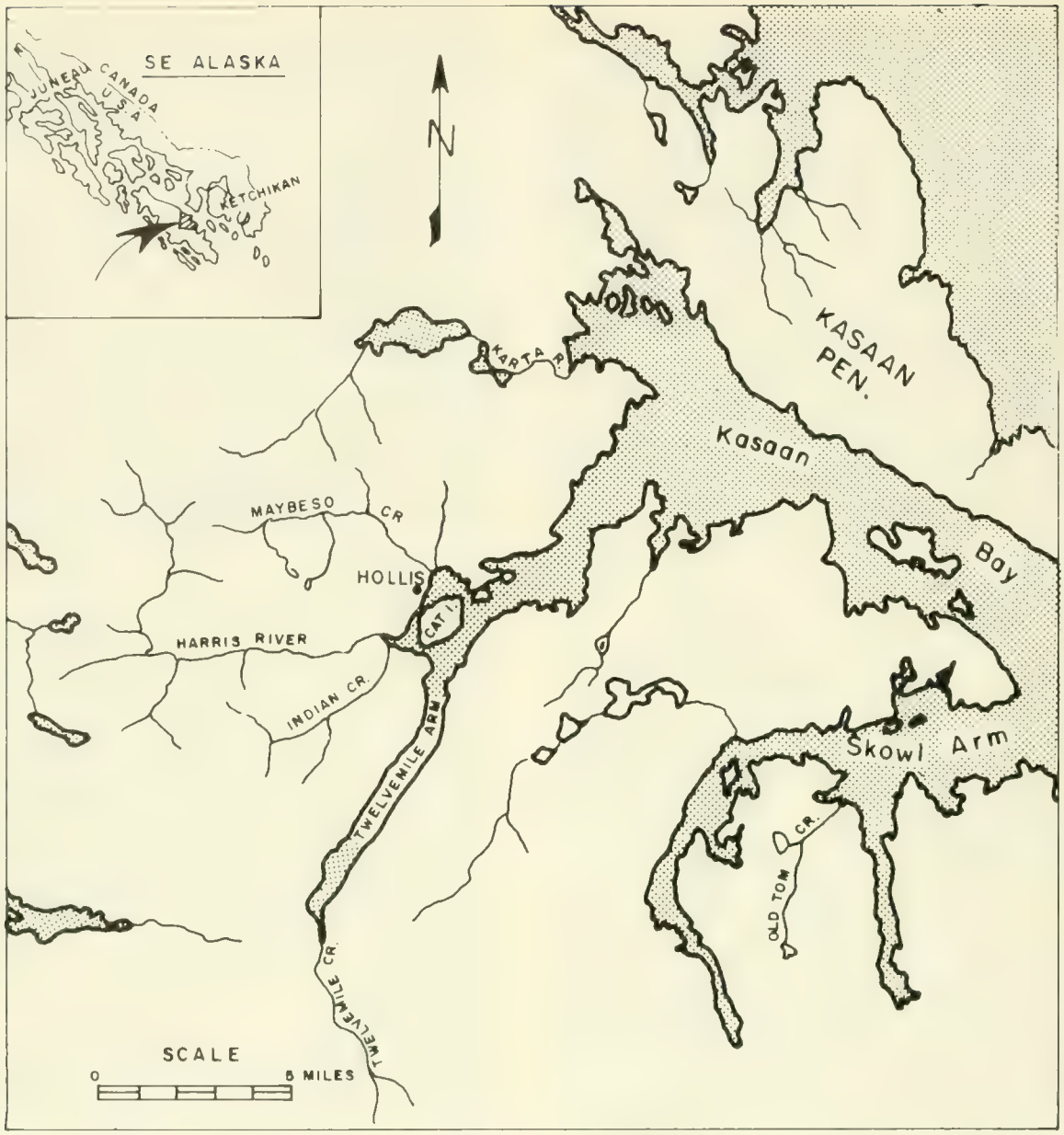

FIGURE 4.—Locations of study streams (Harris River and Indian and Twelvemile Creeks) in the Kasaan Bay region of Prince of Wales Island, Southeastern Alaska.

Field studies began in 1956 when FRI personnel selected six spawning riffles ranging in area from 260 to 650 m.^{2} for sampling. Spawning riffles were sampled in 1956, 1957, and 1958 to measure mortality of eggs and larvae and the quality of intragravel water (table 1).

The study areas were enlarged in 1958, when FRI personnel selected five spawning areas ranging in size from 3,400 to 13,400 m.^{2} The areas included major spawning grounds of pink and chum salmon in Harris River and Indian and Twelvemile Creeks and incorporated the six spawning riffles previously sampled. The sampling areas were selected to represent both intertidal and upstream areas of the study streams (table 1). Factors measured included density

TABLE 1.—*Size and location of six spawning riffles sampled in 1956, 1957, and 1958 and five spawning areas sampled in 1958, 1959, and 1960*

Study area and years sampled	Tide level	Area
1956, 1957, 1958	*Meters*	*Meters*
Riffle A, Harris River	3.4	305
Riffle B, Indian Creek	4.0	386
Riffle C, Indian Creek	5.2	260
Riffle D, Twelvemile Creek	3.7	648
Riffle E, Twelvemile Creek	4.3	372
Riffle F, Twelvemile Creek	4.9	486
1958, 1959, 1960		
Intertidal Harris River	3.7–4.3	7,800
Upstream Harris River		13,400
Intertidal Indian Creek	3.4–5.2	3,400
Intertidal Twelvemile Creek	3.7–4.9	5,580
Upstream Twelvemile Creek		6,130

and distribution of spawners, mortality of eggs and larvae, quality of spawning beds, and quality of intragravel water.

To insure random sampling, FRI personnel drew maps of areas sampled to scale on cross-sectional paper having 100 squares per square inch. The scale selected made each square representative of not more than a 0.4 $m.^2$ area in the stream. Co-ordinate axes were established for each map, and sampling points were selected by the following procedure. A pair of random numbers was obtained from a random number table—one number for the abscissa and the other number for the ordinate. Distance of the selected square from a reference point and an angle of the selected square from a reference line were measured on the map and recorded for use in the field. When a sample was to be taken, the angle and distance of the sample area were measured from the base line and reference point.

MEASUREMENT OF ENVIRONMENTAL FACTORS

The Northern Forest Experiment Station, U.S. Forest Service, operated a weather station at Hollis, a logging community located within 3 miles of Harris River and Indian Creek spawning areas and within 12 miles of Twelvemile Creek spawning areas (see fig. 4). Forest Service personnel obtained continuous records of air temperature and precipitation during the study. Instruments installed and operated by the Northern Forest Experiment Station recorded water level and temperature of each study stream. Forest Service personnel also established discharge rating curves for each stream. James (1956) gives further information on hydrological studies made by the Forest Service.

Physical quality of the spawning bed was evaluated in each area where observations were made on egg and larval mortality. Environmental attributes measured included the dissolved oxygen content of intragravel water and the size composition and permeability of bottom materials. McNeil (1962b) described the techniques used to measure dissolved oxygen levels and McNeil and Ahnell (1964) described the methods of measuring size composition and indexing permeability of bottom materials.

ESTIMATION OF SPAWNING DENSITY AND POTENTIAL EGG DEPOSITION

Fisheries Research Institute (FRI) personnel estimated the number of female pink and chum salmon occupying study areas by means of daily foot survey censuses when water conditions permitted. Institute personnel also observed tagged females daily to estimate average life on the spawning ground (redd life). Females were tagged before they entered the spawning ground and FRI workers calculated the total number spawning by summing daily abundance and dividing by average redd life; i.e.,

$$\text{Number spawning} = \frac{\sum \text{daily abundance in female days}}{\text{average redd life in days}}$$

A summation of daily abundance was obtained by constructing an eye-fitted curve of the daily counts of females and determining the area under the curve in female days. In the determination of average redd life, daily observations on tagged females have been adjusted to account for the periodicity of observations. Assuming that each tagged female occupied the spawning bed one-half day before being observed the first time and one-half day beyond the date of the last observation, I added 1 day to the duration each tagged female was observed.

Two observers made most of the survey censuses; periodic comparisons of their counts showed consistently good agreement. Although it was not feasible to determine bias in estimates, a recent unpublished study conducted by the author at Sashin Creek revealed good agreement between the number of spawning female pink salmon estimated by this method and the number counted into the stream.

COLLECTION OF EGGS AND LARVAE

Eggs and larvae were collected with a hydraulic sampler (McNeil, 1962a) from small enclosed quadrat or circular areas (sampling units) of known area. Area of sampling units varied from 0.2 to 0.9 m.^{2}

Samples preserved in the field were examined later to determine the number of live and dead eggs and alevins collected. Eggs were preserved in a clearing solution (Stockard's solution).

ESTIMATION OF MORTALITY

Data on egg and larval populations were analyzed by three methods to obtain information on temporal changes and spatial differences in mortality levels. Although the methods have been described (McNeil, 1962a), they will be reviewed briefly here.

Ratio of Dead to Total Eggs and Larvae

Mortality has commonly been estimated from ratios of dead to total eggs and larvae collected in k samples; i.e.,[5]

$$\hat{M}_r = \frac{\sum_1^k \frac{\text{dead}}{\text{live+dead}}}{k} \qquad (3)$$

An estimate of mortality based on such ratios underestimates true total mortality where the number of eggs and larvae present in the spawning bed at the time of sampling is less than the number of eggs originally available for deposition. Despite this limitation, estimates of M_r are very helpful in establishing time of mortality where mortality is caused by factors not associated with the direct removal of eggs and larvae from the spawning bed and are sometimes useful in setting lower limits to total mortality.

Actual and Potential Abundance

Total mortality (M_t) can be estimated from statistics on potential egg deposition and abundance of live eggs and larvae at the time of sampling. In this study, estimates of M_t were calculated from the double inequality

$$1-\frac{\bar{a}}{E'} \leq \hat{M}_t \leq 1-\frac{\underline{a}}{E'} \qquad (4)$$

In double inequality (4), the value $\bar{a}$ and $\underline{a}$ are the upper and lower confidence limits respectively of the estimated number of live eggs and larvae per m.^{2} of spawning bed, and E′ is the expected number per m.^{2} Values for $\bar{a}$ and $\underline{a}$ were calculated with the standard error of the mean obtained from either arithmetic or log-transformed counts of live eggs and larvae. Log-transformed counts are used only if the efficiency of the estimate of M_t is increased without introducing significant bias.

Where the logarithmic transformation is used, each observed count is transformed by the equation

$$b_i = \log_{10}(n_i+\beta) \qquad (5)$$

In equation (5), b_i is the transformed variate and n_i is the number of live eggs and larvae collected at the i^{th} point. The term β is a constant which describes the degree of contagion in a negative binomial distribution. A value of β is calculated from the expected frequency of zero observations in a negative binomial distribution. The method, described by Anscombe (1949) and Bliss (1953), requires an iterative solution of the equation

$$\frac{1}{\beta}\log_{10}(1+\beta\bar{n}) = \log_{10}\left(\frac{k}{k'}\right), \qquad (6)$$

where k is the total number of observations, k' is the number of zero observations, and $\bar{n}$ is the sample arithmetic mean.

To set confidence limits to estimates of abundance of eggs and larvae with log-transformed data, the mean log values must be corrected so that the arithmetic mean will result from the antilog. A correction term is required because the mean of log-transformed data is geometric rather than arithmetic (Ricker, 1958, ch. 11). Jones (1956) developed the correction term and described the method used here to calculate confidence limits with log-transformed counts. The equation used to obtain an arithmetic mean ($\bar{n}$) from the log-transformed counts is

$$\bar{n} = \text{antilog}(\bar{b}+1.1518s_b^2)-\beta, \qquad (7)$$

where $\bar{b}$ is the logarithmic mean value and s_b^2 is the sample variance of the log-transformed counts. The term β is subtracted to correct for its addition to the counts before making the transformation in equation (5).

[5] The value $\hat{M}_r$ estimates the population parameter M_r. The circumflex and tilde will be used to identify estimators of other population parameters.

Provided the estimates $\bar{a}$, $\underline{a}$, and E' are unbiased, double inequality (4) gives an unbiased estimate of the total mortality fraction from the time of spawning to the time of sampling. Absence from the spawning bed of dead eggs and larvae does not introduce bias to estimates of M_t as it does to estimates of M_r based on ratios of dead to total eggs and larvae present.

Potential egg deposition (E) is calculated by multiplying the estimated number of female salmon spawning within each area by average fecundity. The value E' is obtained by multiplying E by a factor correcting for the fraction of eggs and larvae present within the streambed actually collected. In the present study, the relationship

$$E' = \frac{9}{10} E \qquad (8)$$

is used. Methods used to obtain the correction term, $\frac{9}{10}$ are described elsewhere (McNeil, 1962a).

More recent studies provide evidence that estimates of M_t obtained with a hydraulic sampler are fairly representative of the true total mortality fraction. I used a hydraulic sampler to estimate total mortality of 1961 and 1963 brood year preemergent pink and chum salmon fry in Sashin Creek, where total fresh-water mortality also was calculated from weir counts of adults entering and fry leaving the stream. In Sashin Creek, it was assumed that $E' = \frac{93}{100} E$ for purposes of setting confidence limits to M_t. Based on samples of preemergent fry obtained with a hydraulic sampler, confidence limits of M_t bracketed the total mortality fraction calculated for each species and brood year from weir counts. In each instance, mean estimated mortality from sampling preemergent fry and from counting migrant fry differed by less than 2 percent. The results are summarized in table 2. In Sashin Creek, potential egg deposition was determined by counting adults entering the stream. In Harris River and Indian and Twelvemile Creeks, the methods of estimating potential egg deposition were not as precise, and it is doubtful if estimates of M_t were completely unbiased.

TABLE 2.—*Total mortality of Sashin Creek pink and chum salmon estimated by sampling preemergent fry with hydraulic sampler and by counting migrating fry at weir*

Species and brood year	Mortality estimated by sampling preemergent fry		Mortality estimated by counting migrating fry
	Mean	90-percent confidence limits of the mean	
Pink salmon			
1961	0.777	±0.041	0.790
1963	.800	±.052	.804
Chum salmon			
1961	.928	±.056	.917
1963	.997	±.040	.995

[1] Mortality of the 1962 brood year was not estimated by sampling preemergent fry because populations were very small. Only 4 pink and 42 chum salmon females entered Sashin Creek to spawn in 1962.

Presence or Absence of Eggs and Larvae

Estimates of the population parameters M_r and M_t sometimes fail to differ significantly when other evidence suggests high mortality. A chi-square test helped demonstrate significant mortality in certain of these cases and often proved to be a more sensitive test for detecting time of mortality than the mortality estimates M_t and M_r.

The chi-square test is based on the premise that the proportion of points within a spawning bed occupied by live eggs and larvae varies with total mortality. If no change in mortality occurs, the following conditions will be satisfied: (1) There will be no decrease in the expected fraction of points populated by eggs or larvae (live plus dead); (2) there will be no decrease in the expected fraction of points populated by live eggs and larvae; and (3) there will be no increase in the expected fraction of points populated by dead eggs or larvae.

In this study, each point sampled was classified according to the number of eggs and larvae present, with points containing less than 35 eggs and larvae per m.^{2} (k_0) being classified together. The classes used were (1) less than 35 live plus dead eggs and larvae per m.^{2}, (2) less than 35 live eggs and larvae per m.^{2}, and (3) less than 35 dead eggs and larvae per m.^{2}.

Principal purpose of the classification scheme was to classify jointly all points containing few eggs and larvae and those containing none. The selection of less than 35 per m.^{2} for joint classification was arbitrary, however.

I tested each class independently with chi-square (see Snedecor, 1956), and set confidence limits to the number of points estimated to contain fewer than 35 eggs and larvae per m.^{2} from the normal approximation of the binomial distribution.

The 90-percent confidence limits of k_0 ($\underline{k}_0$ and $\overline{k}_0$) are obtained from the expression

$$(\overline{k}_0,\ \underline{k}_0) = k\hat{p}_0 \pm 1.645[k\hat{p}_0\ (1-\hat{p}_0)]^{1/2} \qquad (9)$$

where k is the number of points sampled and $\hat{p}$ is the fraction of points estimated to contain fewer than 35 eggs and larvae per m.^{2}

OBSERVATIONS ON ENVIRONMENT AND MORTALITY

Although numerous workers have postulated factors causing mortality of eggs and larvae, few have presented quantitative estimates of mortality satisfying three essential criteria: (1) Estimates free of bias, (2) estimates representative of natural populations, and (3) estimates related directly to causative factors. It is not surprising that these criteria have not been met entirely in field studies, for there are many difficult problems requiring solution. In the present study, an effort was made to reduce (or at least recognize) bias in mortality estimates. Furthermore, because of the randomization techniques used, the samples were thought to be representative of the populations studied. However, the difficulties in associating observed mortality levels with their causative factors are formidable even with the first two criteria being satisfied in part. The problem of relating observed mortality levels to causative factors is complicated in most instances because of interactions among environmental factors.

I attempted to account for interactions by classifying environmental factors causing mortality into generally inclusive groupings: (1) Oxygen supply and related factors, (2) stability of the spawning bed, and (3) freezing of intragravel water. I did not consider one inclusive grouping—pathogenic agents.

OXYGEN SUPPLY AND MORTALITY

Environmental requirements of salmon eggs and larvae were briefly reviewed in an earlier section. My purpose here will be (1) to describe the physical characteristics of spawning beds where observations on mortality were made, and (2) to describe the relation between environmental quality (as related to oxygen supply) and the observed mortality levels.

Dissolved Oxygen Content of Intragravel Water

The dissolved oxygen content of intragravel water was consistently lower at the beginning than at the end of the spawning period in all study streams. There also were observed spatial differences in mean dissolved oxygen levels among and within the study streams.

In late August, at the beginning of spawning, oxygen levels appeared to be lowest in the intertidal Harris River and the upstream Twelvemile Creek spawning areas and highest in the upstream Harris River and the intertidal Indian Creek and Twelvemile Creek spawning areas. Near the end of spawning, in late September, differences in mean oxygen levels were no longer significant among the spawning areas sampled. The data are summarized in table 3, and mean values obtained in 1959 are shown in figure 5 to illustrate the kind of relation observed.

Differences among years in mean dissolved oxygen levels were considerably greater than differences among streams. Summer 1957 was of particular interest in this regard because unusually low levels of dissolved oxygen were observed. Average values of all dissolved oxygen determinations made in the study streams near the beginning of spawning over the period 1956

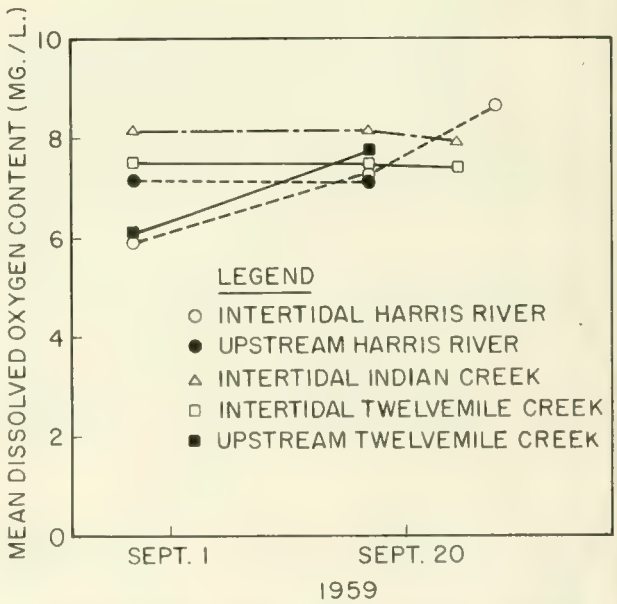

FIGURE 5. Mean dissolved oxygen content of intragravel water in the study streams over the period of spawning in 1959.

TABLE 3.—*Ninty-five-percent confidence interval estimates of mean dissolved oxygen content of intragravel water in study streams*

[Water samples were collected 7 to 10 inches beneath the streambed surface. All values are given as mg./l.]

Date	Harris River		Indian Creek Intertidal	Twelvemile Creek	
	Intertidal	Upstream		Intertidal	Upstream
1958					
Sept. 1	------	------	------	$6.3<\mu<7.4$	$4.8<\mu<6.1$
Nov. 30	------	------	------	$8.3<\mu<9.5$	$8.0<\mu<9.6$
1959					
Aug. 28	$5.1<\mu<7.0$	$6.4<\mu<8.1$	$7.5<\mu<8.9$	$6.8<\mu<8.3$	$5.3<\mu<6.9$
Sept. 17	$5.6<\mu<9.1$	$6.0<\mu<8.4$	$7.1<\mu<9.3$	$6.5<\mu<8.5$	$6.7<\mu<8.4$
Sept. 24	------	------	$7.4<\mu<8.4$	------	------
Sept. 27	$8.1<\mu<9.3$	------	------	------	------
1960					
Aug. 24	------	------	------	$6.8<\mu<8.0$	$5.6<\mu<6.7$
Aug. 25	$5.4<\mu<6.6$	$5.8<\mu<7.0$	$6.3<\mu<7.8$	------	------
Sept. 14	$7.1<\mu<9.0$	------	$7.6<\mu<8.9$	$7.5<\mu<9.0$	$5.4<\mu<7.2$

through 1960 are shown in figure 6. Oxygen levels were severely depressed in 1957, and high mortality of 1957 brood year eggs occurred. The relation between mortality and oxygen levels will be discussed later.

COMPOSITION OF BOTTOM MATERIALS

There were marked differences in size composition of bottom materials among the study streams. The bed of Indian Creek contained greater quantities of coarse materials and smaller quantities of fine materials than the beds of either Harris River or Twelvemile Creek. The bed of Twelvemile Creek contained considerably more silt than the beds of Indian Creek or Harris River. Table 4 lists the average size composition (by volume) of bottom materials in each of the study streams.

The volume of fine materials in salmon spawning beds is inversely related to the permeability of bottom materials (McNeil and Ahnell, 1964). Figure 7 shows the observed relation between the percentage of bottom materials by volume passing through an 0.833-mm. sieve and the coefficient of permeability.

The observed mean percentages of solids passing through an 0.833-mm. sieve are listed below for the study streams in order of decreasing permeability:

	Percent
1. Intertidal Indian Creek	9
2. Upstream Harris River	14
3. Intertidal Harris River	17
4. Intertidal Twelvemile Creek	18
5. Upstream Twelvemile Creek	19

McNeil and Ahnell (1964) found that the finest fractions contained the highest percentages of organic detritus. It will be assumed, therefore,

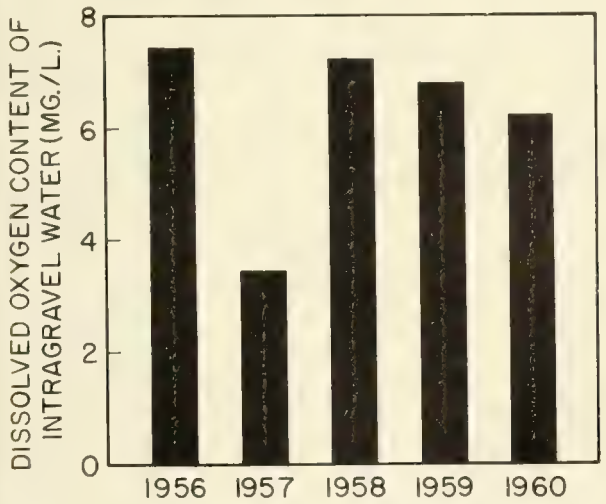

FIGURE 6.—Approximate mean dissolved oxygen content of intragravel water in the three study streams (Harris River, Indian Creek, and Twelvemile Creek) near the beginning of the spawning period (1956–60).

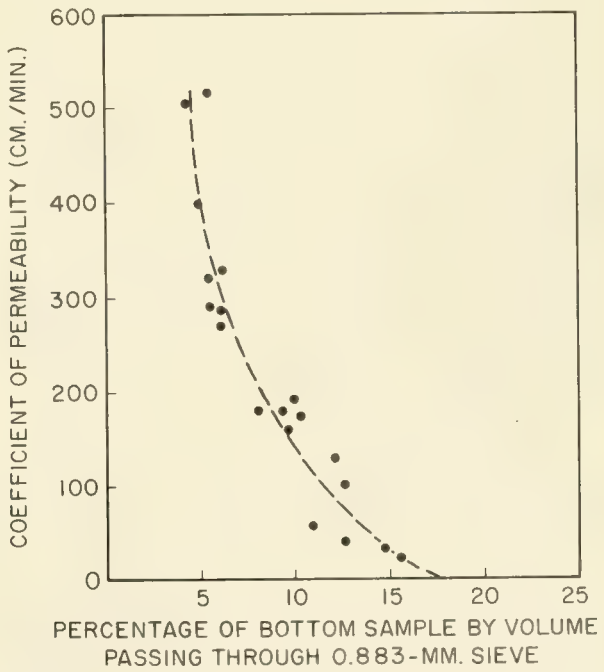

FIGURE 7.—Relation observed between coefficient of permeability and the fraction by volume of a bottom sample passing through an 0.833-mm. sieve (from McNeil and Ahnell, 1964). Curve fitted by eye.

TABLE 4.—*Average size composition of bottom materials in the study streams* [1]

[All rocks larger than 105 mm. diameter have been excluded]

Spawning area	Mean percent of total volume of solids retained by sieves with opening (in mm.) of— [2]									Percent of total volume of solids settling from suspension
	26.26	13.33	6.88	3.33	1.65	0.833	0.417	0.208	0.104	
Harris River (intertidal)	25.1	14.6	13.2	11.0	7.9	11.5	10.5	2.7	0.4	3.1
Harris River (upstream)	24.0	16.2	14.1	11.8	8.4	11.8	9.2	2.4	.4	1.9
Indian Creek (intertidal)	35.2	15.3	12.9	11.3	7.3	8.6	4.9	1.3	.4	2.7
Twelvemile Creek (intertidal)	21.2	15.1	13.9	12.5	8.8	10.7	8.4	2.5	.9	5.9
Twelvemile Creek (upstream)	19.7	13.9	13.0	12.9	9.6	11.6	9.5	3.6	1.2	5.0

[1] For a description of methods of collecting and classifying samples, the reader is referred to McNeil and Ahnell (1964).
[2] Data are taken from table 2 of McNeil and Ahnell (1964).

that the percentage of fine materials obtained from the settling funnel used in the analysis of bottom samples (McNeil and Ahnell, 1964) provides an index of the relative amounts of extraneous organic matter in spawning beds. Percentages of fine materials passing through a 0.104-mm. sieve, observed in the total volume of bottom materials collected from the areas sampled, are listed below in order of increasing values:

	Percent
1. Upstream Harris River	1.9
2. Intertidal Indian Creek	2.7
3. Intertidal Harris River	3.1
4. Upstream Twelvemile Creek	5.0
5. Intertidal Twelvemile Creek	5.9

The rate of interchange between stream and intragravel water is believed to be related to gradient and roughness of the stream bottom. Steep-gradient areas have a greater potential for changes in curvature of the stream bottom than shallow-gradient areas, and coarse materials give greater roughness to the stream bottom than fine materials. To index relative roughness, the study areas are listed below in order of decreasing amounts of solids retained by the largest sieve used in this study (26.26-mm.).

	Percent
1. Intertidal Indian Creek	35
2. Intertidal Harris River	25
3. Upstream Harris River	24
4. Intertidal Twelvemile Creek	21
5. Upstream Twelvemile Creek	20

In addition to having the largest fraction of coarse gravel, Indian Creek also had the steepest gradient (0.7 percent as opposed to 0.2 to 0.4 percent for the other areas). The evidence suggests that the interchange potential of Indian Creek is greater than Harris River or Twelvemile Creek.

Spawning Density

According to the evidence just presented, environmental conditions related to oxygen supply and survival of eggs and larvae would appear to be most favorable in intertidal Indian Creek and least favorable in upstream Twelvemile Creek. The remaining three areas did not appear to vary significantly with regard to the environmental factors evaluated. Observed distributions of spawning female pink and chum salmon appeared to be related to the physical characteristics of the spawning beds studied.

For the years 1958, 1959, and 1960 intertidal Indian Creek had the highest average density of spawners, and upstream Harris River and Twelvemile Creek had the lowest. In order of decreasing average density, the density of spawning females in the sampling areas were estimated to be:

1. Intertidal Indian Creek—mean=35 females per 100 m.^{2} (range 13 to 46 females per 100 m.^{2})
2. Intertidal Harris River—mean=29 females per 100 m.^{2} (range 13 to 48 females per 100 m.^{2})
3. Intertidal Twelvemile Creek—mean=17 females per 100 m.^{2} (range 11 to 25 females per 100 m.^{2})
4. Upstream Harris River—mean=4 females per 100 m.^{2} (range 2 to 6 females per 100 m.^{2})
5. Upstream Twelvemile Creek—mean=4 females per 100 m.^{2} (range 1 to 10 females per 100 m.^{2})

Time and Magnitude of Mortality

The amount of dissolved oxygen required by salmon eggs and larvae for normal metabolism approaches a maximum just before hatching (see fig. 2). After hatching, levels of dissolved oxygen limiting metabolism are greatly reduced, and oxygen requirements are least likely to be satisfied before hatching.

Pink and chum salmon eggs begin to hatch in the study streams in November, and most hatch before mid-December. Figure 8 shows the percentages of live eggs and larvae collected from intertidal Harris River and Indian Creek that had hatched before the date of sampling. Twelvemile Creek is thought to lag 1 or 2 weeks behind Harris River and Indian Creek with regard to time of hatching, because the peak of spawning occurs about 1 week later.

After the spawning period, it is convenient to consider two periods during which mortality occurs—prehatching (autumn) and posthatching (winter). The dissolved oxygen supply and related factors are thought to exert their greatest influence on mortality before hatching, so the discussions here will be limited primarily to mortality of eggs.

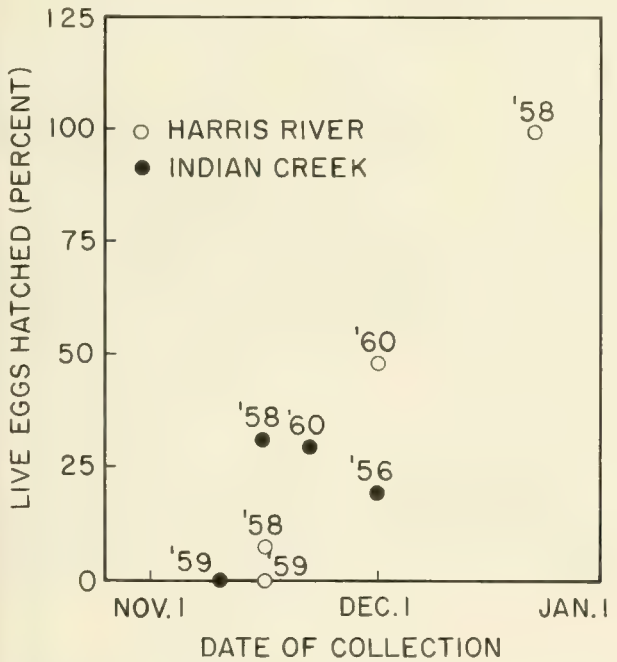

FIGURE 8.—Percentage of live eggs and larvae in collections from intertidal Harris River and Indian Creek hatching before the date of sampling. (Brood years are indicated by numerals.)

In this study, estimates of three population parameters thought to provide evidence of the effect of oxygen supply and related factors on egg mortality were used: (1) Total mortality fraction (M_t), (2) mortality fraction from ratios of dead eggs in samples (M_r), and (3) fraction of points containing fewer than 35 dead eggs per m.^{2} (p_0).

An estimate of M_t includes mortality from all causes, and this estimate includes eggs removed from the spawning bed. Such removal can obscure mortality from causes where there is no direct removal of eggs; therefore, the estimated total mortality ($\hat{M}_t$) was often of limited value in measuring egg mortality from oxygen supply and related factors. Furthermore, estimates of M_t were highly inefficient, and the resulting confidence limits were often broad.

The other two estimates ($\hat{M}_r$ and $\hat{p}_0$) also had limitations imposed by the disappearance of eggs from the spawning bed. Disappearance from gravel shift alone would have little effect on validity of estimates of ratios of dead to total eggs present in the streambed ($\hat{M}_r$), provided live and dead eggs disappear in numbers proportional to their abundance. On the other hand, losses from decomposition and scavenging affect only dead and dying eggs and would cause mortality to be underestimated by $\hat{M}_r$.

Use of the number of points where eggs were present or absent to index occurrence of mortality also would be affected by disappearance because evidence of mortality from factors not related to the direct removal of dead eggs would have been destroyed. Major losses due to gravel shift would tend to invalidate the use of $\hat{p}_0$ to detect significant mortality possibly caused by oxygen supply and related factors.

With these possible limitations in mind, the estimates of M_t, M_r, and p_0 are used to evaluate prehatching mortality of the 1956–60 brood years in the three study streams. Each brood year will be considered separately.

1956 Brood Year

Sampling was confined to spawning riffles A (Harris River), B and C (Indian Creek), and D and E (Twelvemile Creek). Workers sampled the riffles in late November 1956 and in late February

TABLE 5.—*Estimated mortality of 1956 brood year pink and chum salmon eggs and larvae based on ratios of dead to total specimens collected*

Stream [1]	Fraction of dead eggs in late November ($\hat{M}_r$)		Fraction of dead eggs and larvae in late February ($\hat{M}_r$)		Estimated fractions of eggs and larvae dying—		
	Mean	90-percent confidence limits of the mean	Mean	90-percent confidence limits of the mean	Early	Shortly before hatching	After hatching
Harris River	0.27	±0.06	0.50	±0.14	0.27	0.14	0.09
Indian Creek	.10	±.04	.75	±.10	.10	.54	.11
Twelvemile Creek	.27	±.06	.41	±.10	.27	.12	.02

[1] All samples were collected from intertidal riffles.

1957. Since spawning density was not estimated in 1956, no estimates of M_t are given. Also, because of small sample size, it is not possible to give meaningful estimates of p_0. Thus, for the 1956 brood year, only estimates of M_r are given to indicate time and magnitude of mortality (table 5).

In autumn 1956, egg mortality appeared to be highest after embryos had eyed. The February sample included three general categories of dead specimens: (1) Embryos dying early (as evidenced by the opacity and advanced decomposition of the eggs), (2) embryos dying just before hatching (as evidenced by development of body structures), and (3) larvae dying after hatching. Table 5 gives estimates of the fractions of total deaths occurring early, shortly before hatching, and after hatching.

Two features of these data stand out. First, early egg mortality was lowest in intertidal Indian Creek ($\hat{M}_r=0.10$ versus $\hat{M}_r=0.27$ in intertidal Harris River and Twelvemile Creek). Second, this relation had reversed by late February. Other evidence, which will be considered later, strongly suggests that freezing was the major cause of mortality of the 1956 brood shortly before and after hatching.

With regard to early egg mortality possibly associated with oxygen supply and related factors, evidence from 1956 brood year embryos does not contradict the possibility that intertidal Indian Creek provides a more suitable environment than either intertidal Harris River or Twelvemile Creek.

1957 Brood Year

Estimated mortality of the 1957 brood year provided the most striking evidence obtained in the course of these studies on relation between oxygen supply and egg mortality. As shown in figure 6, mean dissolved oxygen levels during the spawning period in 1957 were less than 50 percent of other years. These low levels of dissolved oxygen occurred during a prolonged period of low precipitation and discharge. For example, between August 10 and September 25, discharge of Indian Creek exceeded 20 c.f.s. only 30 percent of the time. Also, over this period very low discharge (4 to 10 c.f.s.) prevailed for 2 weeks during and after spawning. Furthermore, clear skies prevailing over the latter half of September were thought to have contributed to an unusually prolific growth of periphyton observed on the surface of streambeds at the time.

The escapement of adults was the lowest observed during these studies. The density of adult female pink and chum salmon spawning in intertidal areas of the study streams was five or less per 100 m.^{2}. The period of spawning lasted only from about September 7–17, the briefest period observed.

There was good evidence that egg mortality was high after spawning in 1957. Eggs were collected from riffles B and C in intertidal Indian Creek and riffles E and F in intertidal Twelvemile Creek during early November 1957 and late March 1958 and from intertidal Harris River in early April 1958.

Because differences in estimated values of M_r were not significant among the study riffles sampled, samples collected from intertidal Indian and Twelvemile Creeks were pooled by date to give the following single estimates of M_r and their 90-percent confidence limits:

$$\text{November } \hat{M}_r=0.69\pm0.19$$

$$\text{March } \hat{M}_r=0.57\pm0.24$$

Difference between the two estimates is not sig-

nificant. The data indicate that mortality was high before hatching and low after hatching.

Most dead eggs collected in November already had decayed considerably and were classified as fragments, suggesting that mortality occurred shortly after spawning. This finding would not be unexpected because dissolved oxygen levels were unusually low during spawning. Furthermore, there was evidence of high biochemical oxygen demand continuing well into autumn 1957. Although oxygen levels had increased significantly between August and November 1957, they were still lower in November 1957 than in August 1958, even though water temperatures were about 6° C. cooler in November 1957 than in August 1958 (McNeil, 1962b).

The high percentage of fragments among dead specimens collected from intertidal Indian and Twelvemile Creeks in November 1957 remained virtually unchanged through March 1958. The values were:

Indian Creek

Riffle B: 92 percent in November and 96 percent in March.

Riffle C: 70 percent in November and 70 percent in March.

Twelvemile Creek

Riffle E: 66 percent in November and 76 percent in March.

Riffle F: 97 percent in November and 95 percent in March.

This was nearly conclusive evidence that estimates of M_r obtained from egg fragments alone would be little changed over late autumn and winter, and estimates of M_r based on presence of egg fragments and made in early spring 1958 would give essentially the same result as estimates made the previous autumn.

Intertidal Harris River was sampled about April 1, 1958, when egg fragments or live larvae were collected at 34 points. Only egg fragments were found at 31 of the 34 points, giving minimal estimates of

$$M_t \geq M_r = 31/34 = 0.91$$

The available evidence suggested that conditions in 1957 were unfavorable for egg survival, and exceptionally high egg mortality occurred in all study streams. This high mortality was associated with unusually low levels of dissolved oxygen in intragravel water and low density of spawners. Unexpectedly low levels of dissolved oxygen prevailed into November 1957, suggesting that the biochemical oxygen demand was unusually high. There is a possibility that the density of females spawning (five or less per 100 m.^{2}) was too low to remove accumulated organic detritus from spawning beds in quantities sufficient to reduce materially the biochemical oxygen demand (Ricker, 1962; McNeil and Ahnell, 1964).

1958 Brood Year

Adult escapements were moderately low in 1958, though considerably higher than in 1957. Spawning densities ranged from 13 females per 100 m.^{2} in intertidal Harris River and Indian Creek to 1 and 2 females per 100 m.^{2} in upstream Twelvemile Creek and Harris River, respectively. Density of spawning females in intertidal Twelvemile Creek was 11 per 100 m.^{2}

Hydrological conditions during spawning favored a higher egg survival than in 1957. Indian Creek maintained discharges of 10 c.f.s. or more over the spawning period as opposed to a minimum discharge of 4 c.f.s. during spawning in 1957, when high early egg mortality occurred.

Observations on mortality were made in intertidal Harris River, Indian Creek, and Twelvemile Creek. Spawning densities in upstream Harris River and Twelvemile Creek were too light to warrant investigations in these areas. Table 6 summarizes the results of the mortality estimates.

For purposes of the present discussions, intertidal Twelvemile Creek can be dismissed because of extreme high early mortality ($\hat{M}_t$=0.97 by late November) apparently caused by scouring during floods, which physically removed eggs from the spawning bed.[6] As a consequence, there were insufficient numbers of eggs remaining to relate observations on mortality to observations on factors affecting oxygen supply. Workers resampled the area in December primarily to check the results of the November sampling.

The numbers of eggs collected approached expectation in intertidal Harris River and Indian Creek. Indian Creek was sampled on one

[6] Potential egg deposition in intertidal Twelvemile Creek during September 1958 was estimated to be 175 per m.^{2} By late November, mean density of live plus dead eggs was estimated to be only four per m.^{2}; by late December only one per m.^{2}

TABLE 6.—*Estimates of* M_t, M_r, *and* p_0 *used to evaluate time and magnitude of mortality of 1958 brood-year eggs*

Spawning area and date	$\hat{M}_t$		$\hat{M}_r$		$\hat{p}_0$	
	Mean	90-percent confidence limits of the mean	Mean	90-percent confidence limits of the mean	Mean	90-percent confidence limits of the mean
Intertidal Harris River:						
Sept. 18	0.26	[1] ±0.25	0.01	±0.01	1.00	
Nov. 15	.51	[1] ±.35	.16	±.23	.96	±0.06
Dec. 20	.84	±.21	.66	±.38	.82	±.12
Intertidal Indian Greek:						
Nov. 15	0	[1] ±.39	.13	±.13	90	±.07
Intertidal Twelve mile Creek:						
Nov. 30	.97	±.04			1.00	
Dec. 28	.99	±.01			1.00	

[1] These estimates of M_t were obtained with log-transformed data.

occasion only (mid-November), and comparisons between the two areas will be limited to the mid-November samples.

The expected number of eggs based on potential deposition was 201 per m.^{2} in both intertidal Harris River and Indian Creek. In mid-November the difference between mean estimates of M_r ($\hat{M}_r$=0.16 in intertidal Harris River, and $\hat{M}_r$=0.13 in intertidal Indian Creek) was not statistically significant. Furthermore, a comparison of values of $\hat{p}_0$ in November gave a chi-square value of 0.46 (1 d.f.), indicating no significant difference in the frequency of occurrence of dead eggs in intertidal Harris River and Indian Creek. Hence, for the 1958 brood year, there was no conclusive evidence of higher egg mortality in intertidal Harris River than in intertidal Indian Creek. It is noteworthy, perhaps, that in intertidal Harris River $\hat{M}_r$ increased significantly between mid-November and mid-December. It is not known if a similar increase occurred in intertidal Indian Creek.

1959 Brood Year

Density of spawners was highly variable among and within the study streams in 1959. Estimated densities of females spawning were:

Intertidal Harris River..... 25 females per 100 m.^{2}
Upstream Harris River..... 6 females per 100 m.^{2}
Intertidal Indian Creek ..... 46 females per 100 m.^{2}
Intertidal Twelvemile Creek.. 15 females per 100 m.^{2}
Upstream Twelvemile Creek.. 1 female per 100 m.^{2}

Because of the very low density of spawning adults, mortality was not studied in upstream Twelvemile Creek, but observations on mortality were made in upstream Harris River. High stream discharge occurred during spawning, providing more favorable conditions for egg survival during spawning than in 1957. Results of studies on mortality of the 1959 brood year are summarized in table 7.

As observed in 1958, mortality in intertidal Twelvemile Creek was very high initially and apparently was associated again with the direct removal of eggs from the spawning bed. Since estimates from upstream Harris River indicated

TABLE 7.—*Estimates of* M_t, M_r, *and* p_0 *used to evaluate time and magnitude of mortality of 1959 brood year eggs*

Spawning area and date	$\hat{M}_t$		$\hat{M}_r$		$\hat{p}_0$ [1]	
	Mean	90-percent confidence limits of the mean	Mean	90-percent confidence limits of the mean	Mean	90-percent confidence limits of the mean
Intertidal Harris River:						
Oct. 6	0.27	±0.24	0.08	±0.06	0.97	±0.03
Oct. 20	.35	[2] ±.21	.11	±.09	.89	±.07
Upstream Harris River:						
Nov. 4	.73	±.23	.17	±.33	.99	±.01
Intertidal Indian Creek:						
Oct. 10	.52	±.18	.08	±.07	.96	±.04
Nov. 10	.27	±.29	.02	±.01	.90	±.08
Intertidal Twelve-mile Creek:						
Oct. 27	.95	±.07			1.00	

[1] $\hat{p}_0$ = the fraction of points containing fewer than 35 dead eggs per square meter
[2] This estimate of M_t was obtained from log-transformed data.

much the same thing, these areas proved to be of little value in evaluating relations between mortality and oxygen supply.

Differences in mortality level between intertidal Harris River and Indian Creek could not be demonstrated with estimates of M_r and M_t. However, estimates of p_0 made in mid-October showed that samples containing 35 or more dead eggs per m.^{2} occurred with almost equal frequency in intertidal Harris River and Indian Creek despite much lower spawning density in intertidal Harris River (about 53 percent of intertidal Indian Creek). This evidence suggested that egg mortality was higher in intertidal Harris River than in intertidal Indian Creek.

1960 Brood Year

Egg mortality was studied in intertidal Twelvemile Creek, Harris River, and Indian Creek (table 8).

High early mortality from causes associated with the direct removal of affected specimens from the spawning bed occurred in intertidal Twelvemile Creek for the third year. In 1960, however, most of this high mortality occurred during spawning ($\hat{M}_t$=0.71 in late September).[7] Since mortality from causes associated with spawning (e.g., redd superimposition) is beyond the scope of this paper, these causes will not be considered further here. By late November there was evidence of increased egg mortality in intertidal Twelvemile Creek, but this mortality was relatively low.

The density of females spawning in intertidal Harris River and Indian Creek was relatively high and nearly equal. Late in September at the conclusion of spawning, estimates of M_r and p_0 were very nearly the same for these two areas. At hatching, however, 35 or more dead eggs per m.^{2} were found at 26 percent of the points sampled in intertidal Harris River and at only 10 percent of the points sampled in intertidal Indian Creek. Estimates of $\hat{M}_r$ also indicated that mortality of eggs remaining in the streambed was higher in intertidal Harris River than in intertidal Indian Creek.

[7] This same phenomenon was also observed in 1961 (unpublished data, FRI, University of Washington, Seattle).

STABILITY OF THE SPAWNING BED AND MORTALITY

Two factors causing gravel to shift in spawning beds are flooding and females digging redds. The importance of redd superimposition as a factor limiting production of salmon fry is beyond the scope of this paper and will not be considered. My discussions will be limited to the influence of flooding and debris movement on egg and larval mortality.

Mortality caused by gravel shift would make itself evident by complete disappearance of eggs and larvae from spawning beds. Changes in abundance and distribution of eggs and larvae will be examined to obtain evidence of mortality caused by gravel movement. Three population parameters will be considered in evaluating the stability of spawning beds: (1) Total mortality (M_t), (2) mean abundance of eggs and larvae per m.^{2} (live plus dead)($\bar{P}$), (3) fraction of points containing fewer than 35 live plus dead eggs per m.^{2} (p_0').

High discharge occurs most frequently in Southeastern Alaska streams during October, November, and December. Autumn storms are often accompanied by heavy rain which sometimes

TABLE 8.—*Estimates of* M_t, M_r, *and* p_0 *used to evaluate time and magnitude of mortality of 1960 brood year eggs*

Spawning area and date	$\hat{M}_t$		$\hat{M}_r$		$\hat{p}_0$ [1]	
	Mean	90-percent confidence limits of the mean	Mean	90-percent confidence limits of the mean	Mean	90-percent confidence limits of the mean
Intertidal Harris River:						
Sept. 28	0.29	±0.18	0.03	±0.01	0.92	±0.05
Dec. 2	.69	±.09	.18	±.07	.74	±.07
Intertidal Indian Creek:						
Sept. 22	.44	±.20	.05	±.05	.91	±.05
Nov. 22	.50	±.22	.12	±.08	.90	±.06
Intertidal Twelve-mile Creek:						
Sept. 30	.71	±.17	.02	±.03	.98	±.02
Nov. 30	.75	[2] ±.08	.11	±.11	.92	±.03

[1] p_0 is the fraction of points containing less than 35 dead eggs per square meter.
[2] This estimate of M_t was obtained with log-transformed data.

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TABLE 9.—*Dates on which rain*[1] *at Hollis, Alaska, exceeded 4.0 inches in 72 hours, 1956–60*

Dates precipitation exceeded 4.0 inches in a 72-hour period	Amount
1956	*Inches*
None	
1957	
Nov. 21–23	4.08
1958	
Oct. 19–21	6.79
Oct. 28–31	5.08
Nov. 7–9	4.14
1959	
Nov. 5–7	5.32
Dec. 5–7	7.02
1960	
Oct. 9–11	4.31
Oct. 20–22	4.08

[1] Data provided by Northern Forest Experiment Station, U.S. Forest Service, Juneau, Alaska.

continues over several days. To index periods of heavy precipitation, dates on which total precipitation exceeded 4 inches in 72 hours at Hollis (fig. 4) are given in table 9. Stream discharge records revealed that unusually high discharges accompanied rainfall of this high intensity. The analysis showed that rain was most intense in 1958 and 1959 and least intense in 1956 and 1957.

Although a comprehensive evaluation of mortality of 1956 and 1957 brood year eggs and larvae was not feasible because of limited sampling, estimates of M_t obtained for these brood years (and discussed previously) gave no indication of losses occurring from spawning beds. Observations on subsequent brood years (1958 and 1959 particularly) have shown, however, that gravel movement during high discharge is an important cause of mortality in the study streams.

1958 Brood Year

Rainfall exceeded 4.0 inches in 72 hours three times between October 19 and November 9, 1958 (table 9). Samples of eggs were collected before and after the storms in intertidal Harris River and after the storms in intertidal Indian and Twelvemile Creeks (table 10).

The number of eggs ($\bar{P}$) estimated to be present in intertidal Harris River near the end of spawning agreed with the expected number (E') obtained from the estimated density of females spawning ($\hat{\bar{P}}=189$ and $E'=201$ per m.^{2}). After the three periods of heavy rainfall, the abundance of eggs had decreased significantly, and the fraction of points containing fewer than 35 eggs per m.^{2} had increased significantly ($X^2=5.5$, 1 d.f.). This was good evidence that a significant mortality attributable to gravel movement had occurred.

In Indian Creek, the number of eggs estimated to be present in November after the storms agreed with the expected number ($\hat{\bar{P}}=222$ and $E'=202$ eggs per m.^{2}); hence, there was no evidence of mortality from gravel movement in intertidal Indian Creek.

The number of eggs estimated in intertidal Twelvemile Creek after heavy rainfall was con-

TABLE 10.—*Estimates of the population parameters* E′, $\bar{P}$, p'_0, *and* M_t *used to evaluate mortality of 1958 brood year eggs possibly caused by movement of bed materials*

Spawning area and date of observation	Number of occasions precipitation was more than 4 inches in 72 hours	Number of dead plus live eggs per m.^{2} (E' and $\hat{\bar{P}}$)		Fraction of points containing fewer than 35 eggs per m.^{2} ($\hat{p}'_0$)		Total mortality ($\hat{M}_t$)	
		Mean	90-percent confidence limits of the mean	Mean	90-percent confidence limits of the mean	Mean	90-percent confidence limits of the mean
Intertidal Harris River:							
September 18		[1] 189	[2] ±101	0.71	±0.11	0.26	[2] ±0.25
to	3						
November 15		[1] 104	[2] ±74	.83	±.09	.51	[2] ±.35
Intertidal Indian Creek							
September 20		[3] 201					
to	3						
November 15		[1] 223	[2] ±84				
Intertidal Twelvemile Creek:							
September 25		[3] 174					
to	3						
November 30		4	±6				

[1] Estimated number of live plus dead specimens in the spawning bed ($\hat{\bar{P}}$)
[2] These limits were set with log-transformed data
[3] Expected number of specimens based on potential egg deposition (E')

siderably less than the expected number. It was thought initially that high discharge caused mortality; however, samples were not collected before heavy precipitation in 1958, and it will be shown subsequently that high mortality of 1960 brood year eggs in Twelvemile Creek occurred in association with spawning before the storms.

1959 Brood Year

Heavy rainfall occurred in early November and December 1959. The evidence indicated that mortality occurred in association with heavy rain in all areas sampled (table 11).

The intertidal Harris River sampling program was modified slightly in 1959 to evaluate egg and larval losses associated with heavy precipitation. Because a sample taken November 16 did not include the entire area sampled on other dates, comparisons were limited to collections made within the area sampled on November 16. It is for this reason that estimates of M_t given in table 11 differ slightly from the estimates given in table 7 for the same dates. The area sampled on November 16 included 75 percent of the intertidal Harris River spawning area described in table 1.

Trees felled by loggers into upstream Harris River and transported through intertidal Harris River on the crests of two mid-October freshets appeared to cause little or no mortality. Nineteen spruce and hemlock trees, some more than 3 feet in diameter at the base of the trunk and more than 100 feet long, and several large alder trees were known to have floated through the intertidal zone. Estimates of $\hat{\bar{P}}$, p'_0, and $\hat{M}_t$ were nearly the same for samples collected before (October 6) and after (October 20) the presence of floating trees.

There was evidence that mortality occurring in intertidal Harris River between October 20 and November 16 was caused by gravel movements during heavy rain. The total population of eggs was estimated to decline about 50 percent between these dates. Associated with this decline were increases in $\hat{p}'_0$ and $\hat{M}_t$. The period of heavy rain

TABLE 11.—*Estimates of the population parameters* E′, $\bar{P}$, p'_0, *and* M_t *used to evaluate mortality of 1959 brood year eggs and larvae possibly caused by movement of bed materials*

Spawning area and date of observation	Number of occasions precipitation was more than 4 inches in 72 hours	Number of dead plus live eggs per square meter (E' and $\hat{\bar{P}}$)		Fraction of points containing fewer than 35 eggs per square meter ($\hat{p}'_0$)		Total mortality ($\hat{M}_t$)	
		Mean	90-percent confidence limits of the mean	Mean	90-percent confidence limits of the mean	Mean	90-percent confidence limits of the mean
Intertidal Harris River: [1]							
September 26 to October 6	None	[2] 393					
October 6 to October 20	None	[3] 288	±105	0.59	±0.09	0.30	±0.26
October 20 to November 16	1	[3] 323	±138	.58	±.12	.28	±.33
November 16 to February 26	1	[3] 159	[4] ±77	.65	±.18	.64	[4] ±.20
		[3] 169	[4] ±46	.65	±.09	.73	[4] ±.08
Upstream Harris River:							
September 26 to November 4	None	[2] 106					
November 4 to March 3	2	[3] 31	±26	.93	±.05	.73	±.23
		[3] 0				1.00	
Intertidal Indian Creek:							
September 26 to October 10	None	[2] 705					
October 10 to November 10	1	[3] 346	±130	.59	±.09	.52	±.18
November 10 to February 29	1	[3] 530	±206	.51	±.13	.27	±.29
		[3] 24	±18	.91	±.06	.97	±.03
Intertidal Twelvemile Creek:							
October 1 to October 27	None	[2] 229					
October 27 to February 21	2	[3] 11	±17	.99	±.06	.95	±.07
		[3] 1	±1	1.00		.99	±.002

[1] Includes 75 percent of the area described in table 1.
[2] Expected number of specimens based on potential egg deposition (E').
[3] Estimated number of live plus dead specimens in the spawning bed ($\hat{\bar{P}}$).
[4] These limits were set with log-transformed data.

FIGURE 9.—Debris deposited in intertidal Indian Creek by the December 1959 flood.

in early December appeared to result in little additional loss of eggs or larvae from intertidal Harris River.

The period of heavy rain in November was not associated with high egg mortality in intertidal Indian Creek, but the period of heavy rain in December was associated with high mortality of eggs and larvae. After high water had receded in December, large numbers of eggs and larvae scoured from the Indian Creek streambed were observed by workers along the banks. About 90 percent of live eggs and larvae in the intertidal Indian Creek spawning bed at the time of high water in December 1959 were probably destroyed. A factor contributing to this high mortality appeared to be the breaking up of a natural log jam located a short distance above the intertidal Indian Creek spawning area and the subsequent deposition of debris from this jam in the spawning area. Figure 9 shows some of the debris deposited in intertidal Indian Creek. Turbulence created by the stream flowing around this debris was believed to have been mainly responsible for causing the stream to alter its course at several locations, washing out or burying deeply a large percentage of eggs and larvae present.

There was evidence that gravel movement caused high mortality in upstream Harris River. No live or dead eggs or larvae were collected from 68 points sampled in February 1960. Other evidence of widespread gravel movement in upstream Harris River was obtained from studies on size composition of bottom materials. There was a significant reduction in volumes of fine sands and silts in bottom materials during high water in autumn 1959 (McNeil and Ahnell, 1964).

1960 Brood Year

Periods of highest intensity rainfall occurred between October 9 and 22. Intertidal Harris River, Indian Creek, and Twelvemile Creek were sampled in autumn 1960 before and after high water (table 12).

Estimated total abundance of eggs in intertidal Harris River, as in the previous 2 years, declined about 50 percent in association with high water. The mean fraction of points containing fewer than 35 eggs per $m.^2$ increased 0.16 after

TABLE 12.—*Estimates of the population parameters* E', $\bar{P}$, p'_0, *and* M_t *used to evaluate mortality of 1960 brood year eggs and larvae possibly caused by movement of bed materials*

Spawning area and date of observation	Number of occasions precipitation was more than 4 inches in 72 hours	Number of dead plus live eggs per m.² (E' and $\hat{\bar{P}}$)		Fraction of points containing fewer than 35 eggs per m.² ($\hat{p'_0}$)		Total mortality ($\hat{M}_t$)	
		Mean	90-percent confidence limits of the mean	Mean	90-percent confidence limits of the mean	Mean	90-percent confidence limits of the mean
Intertidal Harris River:							
September 22 to September 28	None	[1] 735					
		[2] 538	±132	0.33	±0.08	0.29	±0.18
September 28 to December 2	2	258	±72	.49	±.08	.69	±.09
Intertidal Indian Creek:							
September 21 to September 22	None	[1] 708					
		[2] 436	±146	.52	±.09	.44	±.20
September 22 to November 22	2	[2] 380	±162	.47	±.11	.50	±.20
Intertidal Twelvemile Creek:							
September 28 to September 30	None	[1] 381					
		114	±66	.68	±.11	.71	±.17
September 30 to November 30	2	103	[3] ±31	.68	±.11	.75	[3] ±.08

[1] Expected number of specimens based on potential egg deposition (E').

[2] Estimated live plus dead specimens in the spawning bed ($\hat{\bar{P}}$).

[3] These limits were set with log-transformed data.

heavy precipitation in 1960; while in 1958 and 1959 the increase was about 0.10. The difference between an increase of 0.16 and 0.10, however, was not statistically significant in these instances.

As in 1958 and 1959, on occasions when there was no movement of temporarily stationary debris with high water, eggs and larvae in intertidal Indian Creek apparently suffered little mortality. There was also no evidence of mortality associated with flooding in Twelvemile Creek in 1960, although large numbers of eggs had apparently disappeared before high water.

FREEZING OF INTRAGRAVEL WATER AND MORTALITY

The study streams freeze usually in December, January, and February. Hence, mortality attributable to freezing must occur either during or after hatching.

Maximum daytime air temperatures were used as as index of severity of freezing. Periods when daytime temperatures remained below freezing for two or more consecutive days were determined from air temperature records obtained at Hollis by the Northern Forest Experiment Station (table 13). Freezing was most severe in winters 1956–57 (1956 brood year) and 1958–59 (1958 brood year).

1956 Brood Year

There was evidence of high mortality from freezing in winter 1956–57. Estimates of M_r for the 1956 brood year in each of the study streams are summarized in table 5. Mean values of M_r were found to increase between late November 1956 and late February 1957 as follows:

$\hat{M}_r$=0.27 to $\hat{M}_r$=0.50 in intertidal Harris River.

$\hat{M}_r$=0.10 to $\hat{M}_r$=0.75 in intertidal Indian Creek.

$\hat{M}_r$=0.27 to $\hat{M}_r$=0.41 in intertidal Twelvemile Creek.

TABLE 13.—*Periods of daytime freezing and associated precipitation at Hollis, Alaska 1956–61* [1]

Dates when maximum temperature was less than 0° C.	Mean temperature at 5 p.m.	Precipitation
Winter 1956–57:	°C.	*Inches*
Dec. 3–12	−4°	[2] 0.03
Jan. 7–13	−6°	0
Jan. 20–26	−7°	0
Feb. 22–25	−6°	0
Winter 1957–58:		
None		
Winter 1958–59:		
Jan. 1–8	−5°	0
Winter 1959–60:		
None		
Winter 1960–61:		
None		

[1] Data provided by Northern Forest Experiment Station, U.S. Forest Service, Juneau, Alaska.

[2] Fell as snow, given as inches of rain.

Two classes of dead eggs and larvae not present in November samples were found in February samples: dead eggs with well-developed embryos ready to hatch and dead larvae. Death of eggs containing the well-developed embryos occurred after November sampling and before hatching in December.

This prehatching mortality occurred in conjunction with the December 3 to 12 freezeup. The observed posthatching mortality may have been caused, for the most part, by the subsequent more severe periods of freezing in January and February.

I have already summarized in table 5 the estimated fractions of 1956 brood year eggs and larvae dying early, shortly before hatching, and after hatching. Assuming that mortality at and after hatching was caused by freezing, I estimated mortality of the 1956 brood year from freezing to be about 23 percent in Harris River riffle A, 65 percent in Indian Creek riffles B and C, and 14 percent in Twelvemile Creek riffles D and E.

I visited the study streams during the February 22–25 freeze. Except for an occasional exposed riffle, they were coated with ice several inches thick. Freezing appeared to have a greater effect on Indian Creek spawning beds than on Harris River and Twelvemile Creek spawning beds. I attempted to drive metal rods into the Indian Creek streambed at a number of locations. The gravel was often frozen, particularly where exposed by drying of the stream. Anchor ice also had formed at several points examined.

One important conclusion to be drawn from these data is that mortality associated with freezing was highest in the stream having the lowest minimum discharge (4 c.f.s. in Indian Creek as compared with 12 c.f.s. in Twelvemile Creek and 22 c.f.s. in Harris River).

1958 Brood Year

Freezing occurred after hatching in January 1959. Sampling was undertaken in March 1959 ($2\frac{1}{2}$ months after freezing), and the possibility that larvae killed by freezing had decayed before sampling could not be ignored. Therefore, the best evidence of winter mortality possibly associated with freezing may be estimates of M_t which are summarized in table 14.

In intertidal Harris River, mortality was high before freezing and there was no evidence of additional mortality over winter. Intertidal Indian Creek, on the other hand, experienced high mortality over winter, thus supporting earlier findings with 1956 brood year eggs and larvae. There was no evidence of winter mortality in intertidal Twelvemile Creek, but because of the scarcity of larvae in the spawning bed, it is highly unlikely that mortality would have been detected here.

TABLE 14.—*Estimated total mortality of 1958 brood year pink and chum salmon eggs and larvae before and after freezing in winter 1958–59*

Spawning area and date	$\hat{M}_t$	
	Mean	90-percent confidence limits of the mean
Intertidal Harris River:		
Dec. 20, 1958	0.84	±0.21
Apr. 5, 1959	.62	±.29
Intertidal Indian Creek:		
Nov. 15, 1958	0	[1] ±.39
March 28, 1959	.64	±.28
Intertidal Twelvemile Creek:		
Dec. 28, 1958	.99	±.01
March 24, 1959	.99	±.01

[1] This limit was set with log-transformed data.

Other Brood Years

According to Hollis air temperatures, there were no prolonged periods of freezing that would affect eggs and larvae of the 1957, 1959, and 1960 brood years. An examination of data on mortality revealed little evidence of mortality possibly caused by freezing.

There was no evidence of winter mortality of the 1957 brood year. Prewinter and postwinter pooled estimates of M_r for riffles B, C, E, and F and their 90-percent confidence limits were:

$$\hat{M}_r \text{ (pooled for November)} = 0.69 \pm 0.19$$
$$\hat{M}_r \text{ (pooled for March)} = 0.57 \pm 0.24$$

With regard to the 1959 brood year, there was a rather high incidence (18 percent) of dead larvae in samples collected from intertidal Harris River on February 26, 1960, but a low incidence (less than 1 percent) of dead larvae collected in samples from intertidal Indian Creek. Factors other than freezing probably were responsible for the mortality observed in intertidal Harris River because temperatures were mostly above freezing in winter 1959–60, and few dead larvae were found in intertidal Indian Creek. Scarcity of eggs and larvae in

Twelvemile Creek spawning areas made it impractical to evaluate winter mortality there.

Only a small number (about 1 percent) of 1960 brood year larvae collected in late winter 1961 from intertidal Harris River and Indian Creek were dead. Of 933 larvae collected in intertidal Twelvemile Creek, 9.4 percent were dead, but most dead larvae were found in one redd. Factors other than freezing were suspected of having caused their death.

An experiment indicated that little or no freezing of intragravel water occurred in winter 1960–61. One-half-dram vials were filled with water and buried 5 and 10 inches in spawning beds during autumn 1960. They were recovered in spring 1961 and examined for breakage caused by water expanding during freezing. The recovery of a broken vial was used to indicate occurrence of freezing at the point of burial. Breakage from causes other than freezing was minimized by enclosing vials in latex tubing. Sixty-three vials were recovered from intertidal Indian Creek, 36 from intertidal Harris River, and 30 from intertidal Twelvemile Creek. There were no broken vials in the lot. This experiment provided further evidence that intragravel water did not freeze in winter 1960–61.

DISCUSSION AND CONCLUSIONS

There is evidence that mortality of pink and chum salmon from egg deposition to fry migration is seldom less than 75 percent and commonly exceeds 90 percent in small coastal streams. Freshwater mortality, therefore, may place more severe restrictions on production of pink and chum salmon than natural salt-water mortality.

A thorough understanding of the ecological and physiological requirements of pink and chum salmon eggs and larvae is necessary for evaluating the potential of spawning beds to produce fry. It has been a goal of these studies to determine the relative importance of certain factors affecting quality of the spawning bed environment and fry production.

OXYGEN SUPPLY AND RELATED FACTORS

It is evident from a review of the literature that the oxygen supply rate to an egg or larva is a function of oxygen content and velocity of flow of intragravel water, both of which are affected by a complex of interacting factors. It would appear that oxygen privation is more critical in embryonic than in larval stages. For evaluating mortality possibly resulting from an oxygen deficiency, observations on mortality were based primarily on the population of eggs present in the spawning bed at the time of sampling. Where large numbers of eggs had disappeared from spawning beds before sampling, or where density of females spawning was light, it was not possible with the sampling scheme used to obtain data adequate to evaluate prehatching mortality possibly associated with the availability of oxygen. Inadequate data for the intertidal Twelvemile Creek and upstream Harris River and Twelvemile Creek spawning areas were of limited value in evaluating mortality possibly due to oxygen privation, and observations were made mostly in intertidal Harris River and Indian Creek.

Data on (1) dissolved oxygen content of intragravel water, (2) streambed gradient, and (3) organic content, size composition, and permeability of bottom materials showed more favorable oxygen supply in intertidal Indian Creek than in intertidal Harris River. Furthermore, results of mortality studies suggested that prehatching mortality not associated with the disappearance of eggs was lower in intertidal Indian Creek than in intertidal Harris River. Hence, there was general agreement between observations on physical quality of the spawning bed environment and egg mortality.

An opportunity arose in 1957 to evaluate the relation between prolonged low streamflow during spawning and egg mortality. In this instance, unusually low levels of dissolved oxygen in intragravel water were observed during the spawning period. The evidence relating an exceptionally high egg mortality to low streamflow corroborated the findings of other workers (Brett, 1951; Neave and Wickett, 1953; Wickett, 1958).

In these studies it was not possible to demonstrate a direct dependence of egg mortality and population size. In 1957, when spawning densities were extremely low and egg mortality was unusually high, there appeared to be some justification for suggesting that a minimum number of spawners is required to reduce the overall biochemical oxygen demand through the removal of organic detritus from spawning beds (Ricker, 1962). Additional research will be required to resolve this question.

STABILITY OF THE SPAWNING BED

Instability of the spawning bed was an important cause of egg and larval mortality in the study streams. There was no apparent relation between gravel composition and stability during flooding, and high mortality occurred in spawning beds composed of coarse and fine materials. Change in position of temporarily stationary debris caused gravel movement, but the presence of floating debris had little or no effect on gravel movement.

The influence of temporarily stationary debris on the stability of bottom materials was studied in Maybeso Creek (fig. 4), a stream located near Hollis (Bishop and Shapley, 1963). The results of this study gave further support to relations observed between movement of wood debris and mortality of eggs and larvae in Harris River, Indian Creek, and Twelvemile Creek.

High discharge may be a common cause of mortality among salmonid eggs and larvae. In New Zealand, Hobbs (1937) concluded that floods seldom destroyed salmon and trout redds, but at times accounted for a partial failure of a brood year. At Sagehen Creek, Calif., a flood in December 1955 destroyed brook trout, *Salvelinus fontinalis*, and brown trout eggs, causing the complete failure of the zero age group of these species in 1956 (Needham and Jones, 1959).

Observations on dislodgment of salmon eggs and larvae from British Columbia and Southeastern Alaska streams during flooding also have been reported. After flooding, Withler (1952) found preemergent sockeye salmon fry washed from a tributary of Babine Lake, British Columbia, and Wickett (1959) reported the observation of coho and chum salmon eggs on banks and in bushes along the Qualicum River, Vancouver Island. Floods at Sashin Creek in 1941 and 1943 were thought to have killed many pink salmon eggs and larvae (Hutchinson and Shuman, 1942; Davidson and Hutchinson, 1943).

FREEZING OF INTRAGRAVEL WATER

Although freezing has been considered an important cause of mortality, except for Neave (1947), Smirnov (1947), and Semko (1954), little direct evidence showing freezing to be an important cause of pink and chum salmon egg and larval mortality has been reported. I found that freezing caused high mortality of 1956 brood year eggs and larvae, particularly in intertidal Indian Creek. There was also an indication that the 1958 brood year experienced similar high mortality in Indian Creek. Winters of 1957–58, 1959–60, and 1960–61 were mild by comparison, and there was little or no evidence of mortality from freezing.

It was apparent that freezing exerted the greatest influence on mortality in the stream having the lowest minimum discharge. Further study may reveal that certain spawning areas are unproductive because of low discharge during periods of freezing. There was no evidence of high mortality from freezing during winters that maximum daytime air temperatures remained above 0° C.

SUMMARY

1. The available evidence indicates that high mortality of eggs and larvae greatly limits the abundance of juvenile pink and chum salmon. Proper management of pink and chum salmon fisheries will depend in part on a thorough understanding of the factors affecting the potential of spawning beds to produce fry. Field studies of egg and larval mortality are important because they provide information on time and magnitude of mortality that can be associated with causative factors.

2. In the study streams, egg mortality after the end of spawning seldom exceeded 20 percent in the absence of low levels of dissolved oxygen, freezing, or high water. There was evidence that mortality attributable to oxygen privation was highest where water circulation within the spawning bed was impaired.

3. Low levels of dissolved oxygen in intragravel water as well as high egg mortality occurred with low flow during and shortly after spawning. The resulting mortality of eggs was estimated to vary between 60 and 90 percent in the spawning areas sampled.

4. Movement of bottom materials during high water was an important cause of mortality, which was most severe where temporarily stationary debris shifted position within the flood plain. Mortality from movement of bottom materials was estimated to exceed 90 percent in one instance.

5. Freezing was an important cause of mortality only when maximum daytime temperatures remained below 0° C. for at least 2 consecutive days. Mortality from freezing was highest in the stream having the lowest minimum discharge, and was estimated to approach 65 percent on one occasion.

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CORRECTIONS FOR RECENT ISSUES OF THE FISHERY BULLETIN

VOLUME 63, NO. 3

Page 561, table 11. In the head of second column the M should have a subscript 1, not superscript 1.

Page 562, left column, 6th line from bottom. In the first exponent of the equation for p, the M should have a subscript (M_1).

Page 569, right column, 6th line from bottom. The product quantity 2.894 (1.4577) should be 2.894 (.4577).

Page 659, left column, 2d paragraph. Both x's in equation should read $\bar{x}$.

Page 663, right column, 2d full paragraph, 9th line. The figure is 629,000.

Page 666, right column, last line. Equation should read: $(0.22)(0.04)+(0.78)P_A=0.48$ or $P_A=0.60$.

Page 667, left column, 3d paragraph, 10th line. Should read: to the model given earlier (page 661).

Page 669, right column, 4th and 5th lines should read: the Commander Islands recovery data (appendix table 2).

VOLUME 64:

Page 215, right column. The author Florkin, Marcel, should be moved up 4 lines to appear before the 1934a.

Page 220, figure 197. The scale should read 0 to 5.0.

Page 299, figure 268. Legend should read: Slightly slanted tangential section through the opening and adjacent portion of the ovary of *C. virginica*. Oviduct with two eggs at lower left side. Kidney reservoir at lower right. Ovary follicles at top. Drawn semidiagrammatically from a photomicrograph of a preparation. Kahle, hematoxylin-eosin.

Page 349, figure 329. The identification letters, a through f, should be added below the individual figures starting with upper row and reading from left to right.

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LIFE HISTORY OF THE SPINY DOGFISH

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ABSTRACT

The spiny dogfish, a small shark, is a costly nuisance to commercial fishermen off both coasts of the United States. Data on the species' life history were gathered from the literature and from original studies and assembled in one report as a basis for possible future management. The species reaches a maximum length of 100–124 cm. and a maximum weight of 7–10 kg. The females are slightly larger than the males. Dogfish are known to migrate in large schools and, occasionally, to travel long distances. Tagging studies suggest they move offshore in the winter and inshore in the summer. They are opportunistic feeders with a diet list that includes fishes and crustaceans. Age determinations from interpretation of spine markings indicate the dogfish are long lived with some individuals living for 20 or 30 years. The species is ovoviviparous and mating takes place in the cold months. After a nearly 2-year gestation period, a female gives birth to 3–11 pups, each about 25 cm. long. Natural mortality rate apparently is low, and the species has few natural enemies. In 1944 more than 40 million pounds of spiny dogfish were landed as a source of vitamin A. Today about 2 million pounds are landed. In the United States the species has limited value as an industrial fish and even less value as a food fish. It is edible, however, and is valued as food in some European nations. Management of the spiny dogfish off North America is indicated to reduce the damage it causes to more valuable commercial fisheries.

The spiny dogfish *Squalus acanthias* L., a small shark of the family Squalidae, has been one of the most intensively studied fishes, but one in which extensive knowledge is lacking. The species is studied by college students in zoology, ichthyology, comparative anatomy, and vertebrate taxonomy and is a favorite experimental animal for physiological studies including pharmacological toxicity tests. Few comprehensive biological studies of this fish have been made, however, except for Ford's (1921) study at Plymouth, England, Templeman's (1944) study in Newfoundland, and the studies made by Bonham, Sanford, Clegg, and Bucher (1949) in the State of Washington. In general, most of the published reports represent isolated observations or extremely specific studies. As a result, we know, for example, the function of the rectal gland of the spiny dogfish (Burger and Hess, 1960), but we do not know the wintering grounds of the species; we know the mechanism controlling movements of the spiral intestine (Sawyer, 1933), but we do not know the relationship between the groups of dogfish in any one area.

This paper is an attempt to organize and summarize the available information, to which I have added additional original data from recent studies of the spiny dogfish in the Northwest Atlantic. This report is undoubtedly incomplete, but will serve as a starting point for other studies and help the researcher who is not completely familiar with the literature to interpret future observations.

As a convenient method of handling the information, the various phases of the life history of the fish are taken up in turn. Because the species is distributed throughout the Northern Hemisphere (Bigelow and Schroeder, 1948), I have reviewed reports from both the Atlantic and Pacific Oceans. Some consideration has been given,

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as well, to the role of the spiny dogfish in the commercial fishery.

Much of the information reported here is of interest solely because it adds to man's fund of knowledge about the species; however, some of the information has more concrete implications for our commercial fishermen. This latter consideration has been aptly summed up by Bigelow and Schroeder (1948), who state:

"From a practical aspect the spiny dog in the Western Atlantic is chiefly important because it is undoubtedly more destructive to gear and interferes more with fishing operations than does any other fish—shark or teleost."

DESCRIPTION

The spiny dogfish is typically sharklike in appearance (fig. 1). In Western Atlantic waters it grows to a length of about 50–90 cm. and weighs 3.5–4.9 kg., with a maximum of about 100 cm. and 7.3–9.8 kg. The females are slightly larger than the males (Bigelow and Schroeder, 1953). In the Pacific Ocean, off the west coast of the United States, the males reach a maximum of about 100 cm. and 3.9 kg., while the females reach a maximum of about 124 cm. and 9.8 kg. (Bonham et al., 1949).

The upper part of the fish is slate colored, sometimes tinged with brown, with irregular rows of small white spots on each side. The white spots are generally typical of younger fish and may be lacking on older individuals. A distinguishing feature of this shark is the presence of two sharp spines, one anterior to each dorsal fin, the rear spine longer than the front spine. Halstead (1959) reports that a venom gland is located on

FIGURE 1.—The spiny dogfish, *Squalus acanthias*.

the upper posterior part of each spine. He cites no case histories of injuries, however. The spines presumably are used in defense and are capable of inflicting a painful wound.

Spiny dogfish frequently are confused with the smooth dogfish, *Mustelus canis* (Mitchill), a member of the family Triakidae, although examination of the two species will clearly separate them. The smooth dogfish, as the name implies, lacks the sharp dorsal spines. It is a lighter color than the spiny, although it has great ability to change color to match its surroundings. Above a white sandy bottom it usually is a translucent, pearly shade; over a dark bottom it will have a darker color. Individuals, in general, tend to be larger than spiny dogfish; smooth dogfish are 89–137 cm. long with a few attaining 152 cm. in length. Food of the smooth dogfish is mostly large Crustacea, especially lobsters and crabs, although it also eats small fish such as menhaden and tautog. It is a coastal, warm water species that ranges in the Western Atlantic from Uruguay and southern Brazil to Cape Cod. It is one of the sharks that develops a placental attachment between the embryos and the mother; thus it is truly viviparous. The smooth dogfish is of little concern to commercial fishermen.

DISTRIBUTION

Distribution of the spiny dogfish has been, until recently, somewhat obscured by the question of its specific identity. Many ichthyologists held that there were two distinct species, *S. acanthias* in the North Atlantic Ocean and *S. suckleyi* in the North Pacific Ocean. Bigelow and Schroeder (1948) noted that although it was not entirely clear how the two species were related, they had not obviously differentiated themselves specifically during the period since their ranges had become discontinuous. The prevailing opinion today is that the two populations represent but a single species, *S. acanthias*, which occurs in both the Atlantic and Pacific Oceans (American Fisheries Society, 1960). Briefly, the distribution may be expressed as both sides of the North Atlantic, chiefly in temperate and subarctic latitudes, and also on both sides of the North Pacific, in similar latitudes (fig. 2), with close allies in corresponding latitudes in the Southern Hemisphere. The species is of minor economic importance in the Southeast Atlantic, off the West Coast of Africa, but fairly important in Mediterranean Atlantic waters.[2] It occurs chiefly in continental, as contrasted with oceanic, waters, anywhere between the surface and the bottom down to 165–185 meters (Bigelow and Schroeder, 1948) and has been found as deep as 290 meters (see table 1).

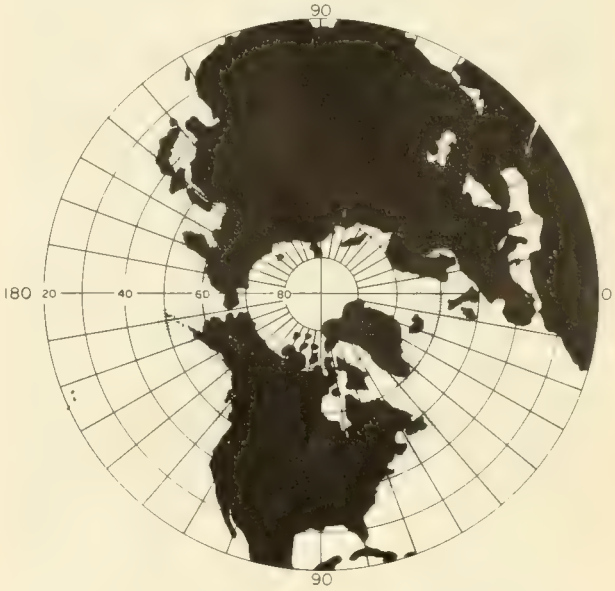

FIGURE 2.—Distribution of the spiny dogfish in the Northern Hemisphere.

The distribution in the Northeast Atlantic is described in detail by Bigelow and Schroeder (1948) as follows: off France, north to Ireland, Scotland, southern Scandinavia, the English Channel, and the North Sea, from there eastward to the Kattegat. The spiny dogfish rarely enters the Baltic Sea. It is plentiful around the Orkney Islands, the Faroes, and south and east of Iceland (but less to the north and west), and is found off Norway to the Murman coast. It is also generally distributed in the Mediterranean Sea and the Black Sea.

In the Northwest Atlantic the spiny dogfish is found in coastal waters from Cape Lookout, N.C., northward around Nova Scotia, along both the northern and southern shores of the Gulf of St. Lawrence, past the Strait of Belle Isle to southeast

[2] Food and Agriculture Organization of the United Nations. 1957. The present status of knowledge of the living resources of the marine waters of the West Coast of Africa. Fisheries Division, Biology Branch, Rome, Italy, 30 pp. [Unpublished processed report.]

Labrador (Bigelow and Schroeder, 1948). It is common northward along the coasts of Newfoundland. There is no record of its occurring along the coast north of Hamilton Inlet. Offshore it occurs in season on Nantucket Shoals, Georges Bank, Browns Bank, the Nova Scotian banks, and the Newfoundland banks. It was also recorded on the west coast of Greenland to Sukkertoppen and Holsteinborg. Hansen (1949) reports that dogfish were formerly a rarity around Greenland, but in the 1930's some were caught in several places on the southwest coast and in the autumn of 1947, around Sukkertoppen.

Local observations of spiny dogfish, and their seasonal occurrence, are reported by Perley (1852), Stafford (1912), Cox (1921), and Jeffers (1932). Each of these authors noted that the appearance of dogfish usually indicated an end of commercial fishing for food fishes.

TABLE 1.—*Water temperature and dogfish catches of 100 or more by otter trawl from research vessels in the Northwest Atlantic from Nova Scotia to the offing of New York, 1948–59*

Date	Depth	Bottom temperature	Catch of dogfish
	Meters	*°C*	*Number*
Feb. 3, 1959	180	9.4	428
Do	152	11.7	367
Apr. 22, 1950	122	9.4	560
Apr. 23, 1950	110	7.2	100
Apr. 26, 1950	219	7.8	103
Do	219	7.2	224
May 1, 1950	189	8.9	372
Do	183	...	1,200
Do	177	8.9	475
Do	201	8.9	269
May 2, 1950	110	4.4	420
May 13, 1950	91	11.1	1,476
Do	91	11.1	152
Do	82	11.1	150
Do	81	5.0	610
May 14, 1950	83	7.2	258
May 15, 1950	142	11.1	110
May 16, 1950	113	7.8	120
Do	85	6.7	140
May 17, 1950	76	5.6	156
June 14, 1955	103	6.1	110
Weighted average	134	8.3	...
July 29, 1949	67	10.6	3,637
Aug. 1, 1950	85	7.8	224
Do	85	8.3	455
Aug. 2, 1950	94	8.9	146
Aug. 5, 1950	293	6.1	234
Aug. 4, 1948	58	6.7	123
Aug. 5, 1948	33	13.3	131
Do	40	11.7	210
Oct. 8, 1958	204	7.8	900
Oct. 9, 1958	222	7.8	122
Oct. 16, 1948	24	12.2	374
Oct. 17, 1948	37	8.3	101
Oct. 20, 1959	55	11.1	1,050
Oct. 30, 1949	74	15.6	248
Do	76	13.3	100
Do	60	14.4	283
Do	55	15.6	115
Oct. 31, 1948	61	15.0	1,561
Nov. 5, 1948	61	14.4	187
Nov. 17, 1956	56	13.3	160
Do	56	16.7	211
Dec. 3, 1948	85		190
Weighted average	85	11.4	

In the Pacific Ocean, Bigelow and Schroeder (1948) report that the spiny dogfish is found on ". . . both sides of the Northern Pacific south to California, Japan, Northern China and the Hawaiian Islands."

MIGRATIONS

The spiny dogfish is a gregarious fish and occurs in schools containing large numbers of individuals. Usually the schools are composed of: (1) very large, mature females; (2) medium-sized individuals, all mature males or all immature females; or (3) small immature individuals of both sexes in about equal numbers (Bigelow and Schroeder, 1953). Hickling (1930), in his studies of spiny dogfish collected off the southern coast of Ireland, noted a relation between the size of the individuals in the schools and the depth of water. Fish of both sexes, from 30 to 45 cm. long, were caught in 55 m., while larger fish of both sexes, from 50 to 89 cm. long, were caught in depths of 164 to 183 m. In general, male dogfish were found in shallower water than females of the same size. The exception to this, however, was for the large pregnant females that were found migrating into shallower water to bear their young.

The appearance of dogfish in our northeastern coastal waters is a rather sudden event. One day, in a given area, there will be fine cod and haddock fishing; the next day there will be nothing but dogfish. They appear as early on Georges Bank (March–April) as they do along New Jersey (March) (Bigelow and Schroeder, 1953). Dogfish are spring and autumn transients only in the southern part of their range, from New York to North Carolina, and in the Cape Cod area they are mostly transients, moving to the north in the spring and to the south in the autumn.

In Newfoundland waters they first begin to appear in June, off the southern end of the island (Templeman, 1944). The largest fish—mature and probably pregnant females—appear first. The mature males appear in the late autumn. As the season progresses, dogfish appear farther northward along the coast and are off Labrador by September. In general, dogfish are plentiful around Newfoundland from June through November or December.

The nature of the dogfish's seasonal migration—coastal north-south, offshore-onshore, or a combi-

nation of the two—is not clearly understood. Part of the problem is the mystery of where the dogfish spends it winters. Bigelow and Welsh (1925) stated, "The winter home of the Gulf of Maine dogfish is still to be learned." They examined the evidence, including the presence of the adults in deep water in Long Island Sound in midsummer, the almost simultaneous appearance of the fish all along the coast north of North Carolina in the spring, and the capture of dogfish by the *Albatross*, February 1920, in 164 to 365 m. along the continental edge off Chincoteague, Va., and off Delaware Bay, and concluded that this ". . . argues for an on-and-off rather than a long-shore migration, with the deep water off the continental slope as their winter home."

More recent evidence of the presence of dogfish in deep water during the winter has been accumulated from observations of dogfish off the Middle Atlantic and New England States (Bigelow and Schroeder, 1936, 1948, 1953). In January 1961, spiny dogfish were taken in an otter trawl by the Bureau of Commercial Fisheries research vessel *Delaware* in 158 to 183 m. along the edge of the Continental Shelf 80 miles south of Martha's Vineyard.

At times, however, dogfish may come into shallow water in the winter. Collins (1883) quotes an item in the newspaper "Cape Ann Advertiser" dated February 10, 1882: "Immense schools of dogfish, extending as far as the eye can reach, have appeared off Portsmouth, an unusual sight in winter."

The accumulated wealth of evidence suggests that temperature governs the seasonal movements of the spiny dogfish. Bigelow and Schroeder (1948) note that dogfish do not appear along the east coast until the water warms to 6° C. and disappear when the water temperature rises to about 15° C. The preferred range of temperature on the offshore wintering grounds seems to be 6° to 11° C.

Survey data (table 1) collected during 1949–59 by the Bureau of Commercial Fisheries Biological Laboratory at Woods Hole indicate dogfish in the Northwest Atlantic prefer bottom water temperatures between 7.2° and 12.8° C. (average, 9.8°). The average temperature at which 100 or more dogfish per haul were caught during the period January–June was 8.3° C.; for the period July–December, 11.4° C.

The survey data also tend to support Bigelow and Schroeder's statement that this species winters in relatively deep water, moving into shoaler water in summer and fall. The average depth at which 100 or more dogfish were caught during the period January–June is found to be significantly different from the corresponding depth for the period July–December (134 and 85 m., respectively).

In Alaska waters incidental catches of spiny dogfish are reported by Hanavan and Tanonaka (1959) during experimental gill netting for salmon. The dogfish were caught in the Bering Sea and in the Gulf of Alaska during July and August when the surface water temperatures ranged from 7° to 13.3° C.

In waters off Japan, Sato (1935) reports an interesting diurnal migration of spiny dogfish. He recorded the body temperatures of dogfish caught in the daytime and at night, on a fishing ground in depths of 110 to 128 m. Thirty dogfish caught at night in a surface drift gill net had body temperatures of from 9.5° to 11.2° C. The surface water temperature at the time was quite similar, from 9° to 12.2° C. In contrast, 28 dogfish caught during the day on a longline on the bottom had body temperatures of from 3.5° to 5.8° C. Unfortunately Sato does not report the water temperature on the bottom. It seems reasonable to assume, however, that the bottom water temperature was within the range of the body temperature of the fish caught on the bottom and that the dogfish were rising to or near the surface at night and descending to the bottom during the day.

In early August 1961, during a cruise of the Bureau of Commercial Fisheries research vessel *Delaware*, dogfish were frequently observed at or near the surface on many of the inshore Gulf of Maine fishing grounds (Robert L. Edwards, personal communication). The water temperatures at the surface were normal for the season (around 15.6° C.), but at the bottom they were abnormally cold (2.8° to 3.9° C. at 73 m.). Few dogfish were taken in the otter trawl at this time.

Edwards (personal communication) observed the dogfish appeared at the surface itself late at night and early in the morning. One morning in Ipswich Bay they were observed to be harrying small schools of euphausiids—as many as six to

eight fish circling each school. The numbers of fish that could be seen at this time were in the thousands. During the day the dogfish retreated to depths of 3 to 5 fathoms. Several hundred were handlined from this depth for tagging and for examining the embryos in the pregnant females. In the late afternoon, occasional fish were again observed at the surface. South of Cape Cod, the dogfish were taken again a few fathoms below the surface. They appeared whenever the otter trawl was hauled in and unwanted fish were discarded.

Edwards, Livingstone, and Hamer (1962) studied the distribution of fishes across the Continental Shelf from Nantucket Shoals to Cape Hatteras. Their results indicate that male spiny dogfish are usually found in cooler water than the females.

Little is known of the salinity preferences of the spiny dogfish. Bigelow and Schroeder (1948), however, note a record of a spiny dogfish that entered a river in Denmark. In their opinion the water was undoubtedly brackish at least near the bottom, rather than fresh, since both cod and *Merluccius* were also present in the river at the same time. Spiny dogfish captured off British Columbia and studied in the laboratory, were able to live for more than 1 hour in distilled water and for nearly 2 hours in tap water (Quigley, 1928a). The author concludes, "Since the dogfish continued to breathe for an average of 113 minutes in tap water and remained active during most of this time, they probably could escape from a freshwater stream even if they were to swim into it above tide water level."

TAGGING STUDIES

Spiny dogfish have been tagged over most of their range by biologists interested in making precise determinations of the migration routes of this fish, and also in learning something of the nature of the dogfish populations. Tag returns from most of the experiments have been at a lower rate than for tagging experiments with commercially valuable fishes; in most fisheries the dogfish is either a nuisance to be avoided or, at best, is retained as a very minor part of the catch. Although many tagged dogfish are undoubtedly recaptured, most are discarded at sea without having their tags noticed; consequently, few tags are recovered. Tagging returns suggest that the dogfish is long lived, for several fish were at liberty for 10 years. Some individual fish migrated long distances.

In a British experiment in November and December 1957, 75 spiny dogfish were tagged with a yellow plastic tab attached with a braided nylon loop (Beverton, Gulland, and Margetts, 1959). The fish were tagged incidentally during a whiting tagging experiment in the northwest part of the Irish Sea. At the time of the report, after 7 months at liberty, only two tagged dogfish were returned despite the fact that originally the dogfish appeared particularly robust and little affected by capture or tagging. No information was given as to the place of recapture of the tagged fish.

One thousand spiny dogfish were tagged near the Shetland Islands, north of Scotland, in November 1958 (Aasen, 1960). The mark used was a yellow slip of polyethylene film with printed text rolled up as a cylinder and attached to the fish with a stainless steel bridle in front of the first dorsal fin. After 2½ months at liberty, 12 tagged fish (1.2 percent) were recaptured, most of them near the west coast of Norway. After 2 years at liberty, 10.8 percent of the dogfish had been recaptured. The returns from this experiment, combined with returns from nearly 3,000 dogfish tagged in later experiments, yielded a combined return rate of 6 percent. Aasen (1962) concluded, "It is obvious that most of the fish migrate towards the Norwegian coast in winter and return to the grounds northwest of the British Isles in summer."

Holden (1962) tagged 278 dogfish in the Irish Sea during 1957–59, and 15 (5.4 percent) were recaptured. Most of the winter recaptures came from the southern part of the Irish Sea, while the summer and autumn recaptures came from Scotland, as far north as the Shetland Islands. Presumably the dogfish wintered in the Irish Sea and migrated to mingle with the Norwegian dogfish north of Scotland in the summer.

Nearly 10,000 dogfish were tagged in the waters off British Columbia and Washington in the 1940's, and 655 (6.7 percent) were recovered (Holland, 1957). In general, the tag returns demonstrated a southward, coastal migration in the autumn and winter and a northward migration in the spring and summer. Several long-distance recaptures were reported from the coastal migrations but the

one outstanding offshore, long-distance migration that was reported was when a dogfish that had been tagged off Willapa Bay, Wash., in 1944 was recaptured near the northern end of Honshu Island, Japan, in 1952. This is a straight line distance of 4,700 miles, but the author concluded that the fish probably followed a great circle route at accustomed depths along the coastal shelf. Longevity of the spiny dogfish is suggested by the above example, a fish at liberty 7 years, and two other fish tagged in the same experiment, which were at liberty 8 years and 10 years, respectively.

Dogfish tagging experiments in the Northwest Atlantic have been reported by Templeman (1954, 1958) for the Newfoundland-Grand Bank area and by Jensen (1961) for the Gulf of Maine-Georges Bank and Browns Bank areas (fig. 3). In the Newfoundland experiment, 279 females were tagged near St. John's in July 1942, and, as of September 1949, 14 fish (5 percent) were recaptured. Many of the tagged fish were caught in the local area and the Maritimes, but two were caught off Gloucester, Mass. (one in 1942 and one in 1943), a distance of 900 miles, and one was caught off Cape Henry, Va., in 1947, a distance of 1,300 miles. The last return was from the Strait of Canso, Nova Scotia, in 1949. Templeman noted (1954), ". . . most of the tagged fish were mature females carrying young and the recaptures show a southward late fall movement of some at least of these large pregnant females, with presumably a compensating northward movement in the spring and early summer." In an earlier report (1944) he suggested that the dogfish migrate rapidly and for long distances in the upper layers of the water.

While the tag returns reported by Templeman indicated a coastwise migration, he did report an astonishing offshore migration from a later tagging experiment (Templeman, 1958). A fish that had been tagged on the southwestern slope of the Grand Bank in June 1947 was recaptured in Faxa Bay, Iceland, in August 1957. The straight line distance between the tagging area and the point of recapture is over 1,300 nautical miles.

Returns of dogfish tagged in the Gulf of Maine area have done little to confirm either a north-

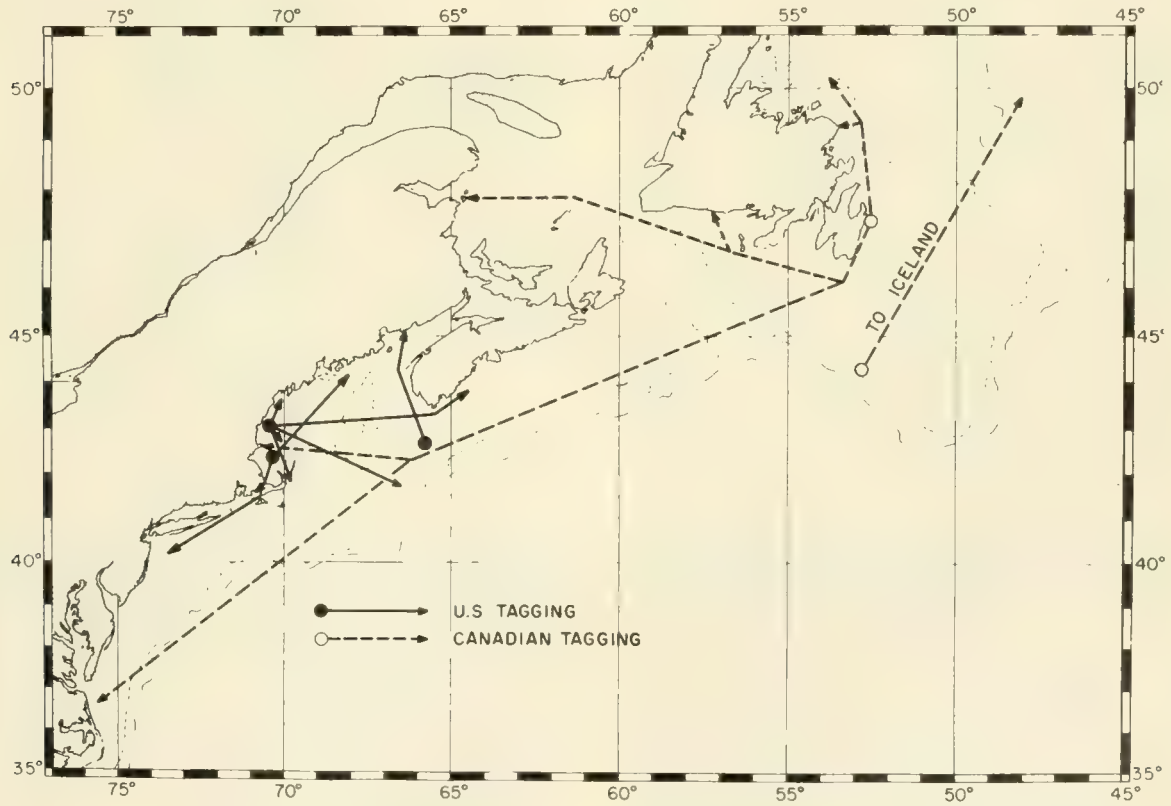

FIGURE 3.—Results of dogfish tagging in the Northwest Atlantic.

south or inshore-offshore migration pattern (Jensen, 1961). In these experiments, 155 dogfish were tagged near Cape Ann, Mass., in July 1956, and 50 were tagged on Browns Bank in October 1957. To date, nine tags have been returned (5.8 percent), eight from the 1956 experiment and one from the 1957 experiment. Most of the tagged fish were recaptured relatively close to the areas in which they had been released; six were caught less than 50 miles from the tagging area; one, 73 miles away; and another, 140 miles away. One, however, at liberty nearly 5 years, was recaptured 200 miles away, on the eastern edge of Georges Bank. In general, the recaptures suggest that spiny dogfish return to the same general area at about the same time of year and the same fish probably school together for long periods of time.

An interesting recapture was made recently of a dogfish tagged in a later series of experiments carried out aboard the *Delaware*. The fish was 1 of 143 caught on handlines in 18 m. of water, July 22, 1961. It was tagged and released 3 miles off Halibut Point, Cape Ann, Mass., and was recaptured by a commercial otter trawler in 119 m. on December 30, 1961, in the vicinity of the Hudson Canyon. The fish had moved about 250 miles in 23 weeks and was caught south and offshore of the tagging area. This recovery adds further evidence to support the hypothesis that some of the dogfish that spend the summer in the inner Gulf of Maine migrate south and offshore to spend the winter.

Table 2 gives the tagging and recapture information for 17 spiny dogfish tagged by personnel of the Bureau of Commercial Fisheries Biological Laboratory at Woods Hole. The 17 represent the returns from a total of 844 dogfish tagged in 1956, 1957, 1960, and 1961.

SEROLOGICAL STUDIES

An approach to the identification of spiny dogfish subpopulations, by blood typing techniques, was made by Sindermann and Mairs (1961). The authors proposed a two-antigen blood group system. They found that individual dogfish collected in the Gulf of Maine were of blood types S_1, S_2, S_1S_2, or S_0. Blood groups of pregnant females and their unborn pups were compatible, " . . . with a simple genetic hypothesis of three alleles, S^1, S^2, and S^0, controlling the system." Continuation of the work, complemented with tagging and other population studies, will make it possible to determine the existence of reproductively isolated subpopulations of spiny dogfish. In addition serological techniques may clarify the relationship between the various *Squalus* species and groups throughout the world.

TABLE 2.—*Returns of tagged spiny dogfish*

Date and locality of—		Time at liberty	Distance
Tagging	Recapture		
		Weeks	*Miles*
July 7, 1956, Boon Island, Maine (43°05′ N.–70°28′ W.).	July 22, 1957, Cape Ann, Mass. (42°44′ N.–70°19′ W.).	54	22
Do	July 29, 1959, Cape Elizabeth, Maine (43°28′ N.–70°12′ W.).	159	26
Do	July 21, 1960, Cape Elizabeth, Maine (43°27′ N.–70°12′ W.).	210	25
July 8, 1956, Cape Ann, Mass. (42°48′ N.–70°15′ W.).	Nov. 15, 1956, Cape Elizabeth, Maine (43°28′ N.–70°10′ W.).	18	40
Do	Mar. 2, 1957, Cape Ann, Mass. (42°38′ N.–70°17′ W.).	34	10
Do	May 22, 1957, Chatham, Mass. (41°40′ N.–69°42′ W.).	48	73
Do	July 16, 1959, Cape Elizabeth, Maine (42°28′ N.–70°10′ W.).	157	40
Do	May 15, 1961, Georges Bank (41°33′ N.–66°35′ W.).	248	185
Do	Sept. 4, 1961, Port Mouton Harbour, Nova Scotia (43°57′ N.–64°38′ W.).	274	280
Oct. 14, 1957, Browns Bank (42°36′ N.–65°46′ W.).	July 12, 1958, Chance Harbour, New Brunswick (44°55′ N.–66°21′ W.).	39	140
July 8, 1960, Stellwagen Bank (42°13′ N.–70°17′ W.).	June 13, 1961, Buzzards Bay, Mass. (41°32′ N.–70°40′ W.).	49	45
May 26, 1961, Woods Hole, Mass. (41°31′ N.–70°40′ W.).	June 11, 1961, Buzzards Bay, Mass. (41°36′ N.–70°50′ W.).	3	9
Do	June 15, 1962, Montauk Point, N.Y. (40°54′ N.–71°39′ W.).	63	64
June 13, 1961, Stellwagen Bank (42°25′ N.–70°21′ W.).	Aug. 22, 1962, Cape Ann, Mass. (42°46′ N.–70°39′ W.).	62	24
July 22, 1961, Cape Ann, Mass. (42°44′ N.–70°36′ W.).	Dec. 30, 1961, Hudson Canyon, (39°41′ N.–72°12′ W.).	23	250
Do	Aug. 24, 1962, Seguin Island, Maine (43°38′ N.–69°37′ W.).	57	71
July 26, 1961, Cape Ann, Mass. (42°46′ N.–70°41′ W.).	Sept. 5, 1961, Portsmouth, N.H. (43°01′ N.–70°41′ W.).	6	15

FOOD HABITS

Several studies of the stomach contents of spiny dogfish from many parts of the Northern Hemisphere have shown that it is primarily a fish eater but will also feed on invertebrates, both swimming and bottom-dwelling forms. In many areas, clupeoids are important in the diet of the dogfish, but it undoubtedly feeds on whatever species it can capture.

In the Pacific Ocean three important studies of dogfish feeding habits have been made. One such

study was conducted to determine the amount of predation, if any, by dogfish on salmon smolts as they descended the Fraser River, British Columbia (Chatwin and Forrester, 1953). In the river mouth, 249 dogfish were examined and 20 (8 percent) had empty stomachs. Of those that contained food, 100 percent contained eulachon (a smelt, *Thaleichthys pacificus*), or traces of it, 5 percent contained sand lance, *Ammodytes*, and 19 percent contained invertebrates, including shrimp, crabs, small crustaceans, squid, and octopus. A large number (21 percent) contained sticks and leaves, no doubt ingested accidentally with the food items. Outside the river mouth, the dogfish diet was much the same: 91 percent eulachon, 29 percent invertebrates, and 5 percent sticks and leaves. Miscellaneous food items included a honeybee and polychaete worms. On the basis of their findings the authors concluded the spiny dogfish was an opportunistic feeder.

Another study in the same general area was made by Bonham (1954) who examined more than 1,100 spiny dogfish stomachs, of which nearly 60 percent contained food. He found more than 77 different food items; fish constituted two-thirds of the diet. The three most common food items were ratfish, *Hydrolagus colliei*, (20 percent); herring, *Clupea harengus pallasii*, (18 percent); and krill, Euphausiidae, (9 percent). The only evidence of cannibalism was the finding of a 230-mm (newborn?) dogfish pup in the stomach of a large pregnant female. Bonham concluded, "Large and small dogfish eat much the same kind of food, with the exception of very small dogfish in whose diet worms and other mud-inhabiting organisms appear prominently."

Sato's (1935) studies of the spiny dogfish in the water around Japan indicate that clupeoids are important in the diet in this area as they are in other parts of the world. He examined the stomach contents of 128 dogfish collected in gill and set nets in June and July. Sixty stomachs contained fish; 48 contained sardines, *Sardinops sagax melanosticta;* and 12 contained other fishes, including herring, *Clupea harengus pallasii*, salmon *Oncorhynchus keta*, and cod, *Gadus macrocephalus*. Invertebrates were found in 21 stomachs.

In waters north of Japan, around Sakhalin, food items found in the stomachs of spiny dogfish were noted by Kaganovskaia (1937). The items were listed simply as herring, iwashi (sardine), cod, octopus, crab, squid, and sea cucumbers.

Food habits of the dogfish in the North Atlantic are quite similar to those of the dogfish in the Pacific. From waters around the British Isles, Ford (1921) reported food items from 143 spiny dogfish with recognizable stomach contents. Fishes were found in 137 stomachs and included herring and pilchard (67 percent), mackerel (19 percent), and gadids (4 percent). Six stomachs contained crustacea, and three had mollusks. The stomachs were collected at a time when the clupeoids and mackerel were abundant and thus readily available to the dogfish.

In the Northwest Atlantic, around Newfoundland, capelin, *Mallotus villosus*, are important in the diet of the spiny dogfish. Templeman (1944) made a casual examination of 24 dogfish stomachs collected in July 1942 and found all of them contained capelin. During this month the capelin were plentiful on the inshore grounds and the dogfish appeared to be feeding almost exclusively on them. He notes, "Some of the stomachs were full of capelin, one containing 13 capelin, 1 of 7 cm. and 12 from 14 to 19 cm. long."

From August to November, Templeman (1944) made a detailed analysis of 1,171 dogfish stomachs of which 665 were empty, 367 contained only the bait used to capture them, and 139 contained food. In the stomachs that contained food, about 60 percent contained fishes, about 45 percent contained Crustacea, about 8 percent contained coelenterates, and a few contained molusks, polychaetes, algae, and miscellaneous items. The recognizable fishes were herring (14 percent), capelin (5 percent), and cod (5 percent).

In the Gulf of Maine, spiny dogfish feed on a wide variety of species and at one time or another prey on practically all species smaller than themselves. They are regarded as the chief enemy of the cod, and also feed on mackerel, haddock, herring, squid, worms, shrimps, and crabs. They are one of the few fishes that eat ctenophores (Bigelow and Schroeder, 1953)

My own observations of spiny dogfish stomach contents have revealed a curious condition in which the stomachs were distended with a clear watery fluid. Casual observations of 50 dogfish stomachs collected during a cruise of the research vessel *Delaware* in June 1961 on Stellwagen Bank re-

vealed fish remains in only three stomachs. Five stomachs contained about 4 ounces of a light-gray, custardlike material, evidently food well advanced in digestion. Most of the stomachs, however, were filled with clear fluid; only a few stomachs were empty and flaccid.

Fifty stomachs examined at Pt. Judith, R.I., in July 1959, contained mostly amphipods (*Leptocheirus*) and occasional fish remains.

In July 1961, John M. Hoberman found silver hake (*Merluccius bilinearis*) in the stomachs of dogfish collected in Ipswich Bay during a cruise of the *Delaware*. Silver hake were abundant in the area at the time.

Fishes and rock crabs (*Cancer*) were the principal food items of 33 spiny dogfish collected in June 1963 off Block Island, R.I. The dogfish were examined aboard the research vessel *Albatross IV*. Sixty percent contained fish, 33 percent contained rock crabs, and 7 percent contained squid. Recognizable food items included squirrel hake, *Urophycis chuss;* silver hake; winter flounder, *Pseudopleuronectes americanus;* and sculpin, *Myoxocephalus* sp.

It is evident spiny dogfish have no food preferences, but eat nearly anything that moves. It is evident too, they are opportunistic feeders, preying on whatever species are abundant and available. Their catholic food habits probably contribute greatly to the species' biological success.

AGE AND GROWTH

The traditional techniques used in fishery biology for age determination are not, unfortunately, applicable to the spiny dogfish. The dogfish does not have scales suitable for examination, and being a cartilaginous fish, it has no true bones in which visible growth zones are formed. Dogfish otoliths, unlike the calcareous otoliths of the teleosts, are simply aggregations of sand particles loosely joined in a gelatinous substance, and thus offer no opportunity for detection of growth zones.

A possible solution to the problem of determining the age of the dogfish is presented in an obscure Russian paper (Kaganovskaia, 1933) read in English translation. Briefly, the paper notes that the dorsal spines of the dogfish are marked with annulations apparently related to growth periodicity (fig. 4). The Russian biologist had collected the dogfish from the waters around Sakhalin. At first she examined the vertebrae, but the barely noticeable rings in them became even less visible after treatment. Cross sections of the teeth and of the dorsal spines were examined, but without success. The teeth showed no zones, and the spines were found to have an internal cavity along their entire length. The enamel coating of the spines, however, had markings, ". . . which doubtless represent annual deposits."

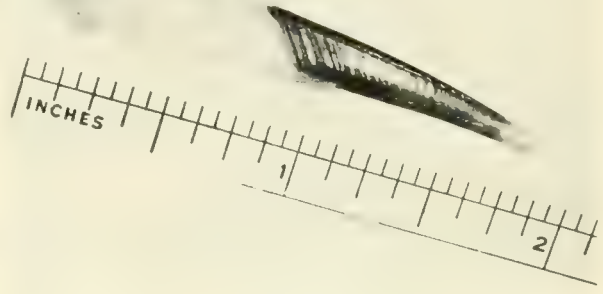

FIGURE 4.—Photograph of a dogfish spine showing the annulations.

The makeup of the spine is quite similar to the makeup of a mammalian tooth. Daniel (1934) describes the structure of the spine as follows:

> For almost half its length the spine is buried in the integument. The buried part is designated as the root or base and the exposed portion the crown or spine proper . . .
>
> . . . The spine contains a large central cavity which when in place fits over a cartilage of the fin skeleton. The walls of the spine are made of dentine which in the crown consists of a double layer. The more superficial layer is bounded anteriorly and laterally by a layer of enamel, but enamel does not extend over the posterior groove which fits up against the basal cartilage of the fin skeleton. A more or less compact layer of pigment . . . separates the enamel . . . in front from the layer of dentine.

Kaganovskaia (1933) did not try to validate the spine markings as year marks although she noted that the spines of fish less than 1 year old were light gray in color and had no markings. She examined a sample of rear dorsal spines (the posterior spines are more clearly marked than the anterior spines) from 210 dogfish, 380–1,180 mm. in length, and reported their ages as 2–25 years.

Her data were presented in a table which I have incorporated into a growth curve (fig. 5). It seems reasonable to consider the spiny dogfish a long-lived species in view of the evidence of tagged dogfish at liberty for up to 10 years.

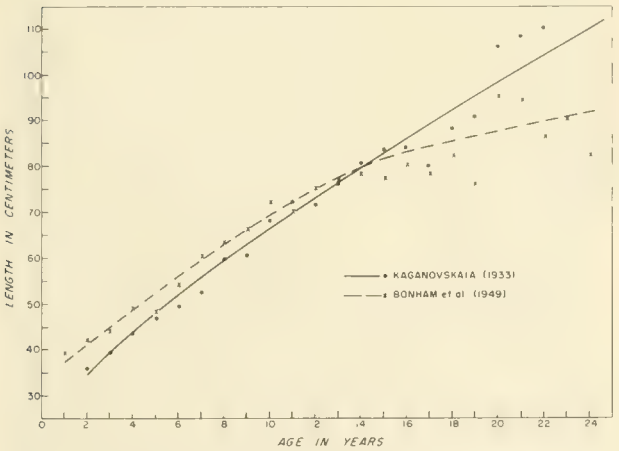

FIGURE 5.—Two growth rates for the spiny dogfish, based on interpretation of spine markings.

Using the Russian method, Bonham et al. (1949) examined the spines from 215 dogfish collected in State of Washington waters. The fish were 34–127 cm. long and 1–29 years old, and although there is variation in the Washington data, the trend is similar to that in the Russian paper. To prepare the spines for reading, Bonham (personal communication) removed them by slicing down along the bases of the spines into the back of the dogfish and freeing the spines from the skin or muscle. The spines were not treated; and low magnification (5X) or none at all was used in actual examination.

Only about 20 percent of the spines (215 out of 1,100) had markings that were sufficiently distinct to be readable without appreciable disagreement by different observers (Bonham, personal communication). In the report (Bonham et al., 1949) the authors cautioned, "It must be understood that rejection of unclear or doubtful spines would probably eliminate from consideration most of the old dogfish, whose spines usually are broken, badly eroded, and have the annulations closely crowded near the bases of the spines."

A recent study by Holden and Meadows (1962) supports the hypothesis of annual zone formation in dogfish spines. The authors examined the spines from dogfish landed by trawlers that fished the grounds around the north and west coasts of Scotland. A total of 317 males (41.3–82.5 cm. long) and 445 females (39.6–97.5 cm. long) were examined. The ages determined were 1–19 years for males and 1–21 years for females. The rate of growth for both sexes was about the same up to the time of sexual maturity (at an age of about 9 years). After the fish became mature, the females grew faster than the males.

Comparisons between dogfish growth calculated from spine readings or length frequencies, and growth observed in tagged dogfish indicate that the growth of the tagged individuals is often half, or less, of the calculated values. Bonham et al. (1949) report that on the basis of a study of eggs and embryos, the suggested rate of growth is 7 cm. in 2 years or about 3.5 cm. per year. The rate calculated from spine readings is 3.1 cm. per year, and from length frequencies 3.3 cm. per year, but from tagging studies the rate is only 1.4 cm. per year.

In the above example, the spine readings were from fish 40–100 cm. long (2.5–21 years, indicated age). An examination of Kaganovskaia's (1933) data for fish of similar lengths and indicated ages suggests a growth of 3.5 cm. per year. Templeman (1944) calculated ". . . approximately 1½ cm. as the average growth per year for all mature females and 1.6 cm. for the first mature year . . ." However, a tagged dogfish at liberty for 10 years grew only about 8.1 cm. in that time (Templeman, 1958), but he concludes the fish was in worse condition when recaptured than when tagged, hence the poor growth rate. Kauffman (1955) reports the growth of two tagged spiny dogfish from the Pacific Coast as 14 cm. after 8½ years at liberty (2.3 cm./year). A dogfish tagged in British Columbia waters and at liberty almost 8 years grew 5⅝ inches (Fisheries Research Board of Canada, 1952), or about 14.1 cm. (1.8 cm./year). My own experience with the growth of tagged dogfish is limited to one specimen at liberty nearly 1 year during which time it grew only 0.7 cm.

At the present time there is no way to resolve the differences reported for the annual growth of the spiny dogfish. No doubt it is a long-lived species, attaining a maximum age of 25–30 years. The lengthy time interval between tagging and recapture, up to 10 years for certain individuals, is

perhaps the strongest evidence supporting the reported age determination studies.

LENGTH-WEIGHT RELATION

As with many fishes, female spiny dogfish grow longer and heavier than the males. Templeman (1944) reported that the immature females are slightly heavier than the males at all sizes. Mature and pregnant females are significantly heavier than either mature males or immature females. He presents a length-weight graph and lists the following lengths and average weights for dogfish from the Newfoundland area:

Length	Weight	
	Males	Mature females
Cm.	*Pounds*	*Pounds*
60	1.7	3.8
75	3.3	5.1
83	4.5	5.1
96		8.4

Pugsley (1939) reported that Pacific dogfish females tend to be heavier per unit of length than males. He includes a length-weight graph that shows this relation for males, females, and pregnant females.

Some length-weight data were collected from 210 dogfish at Point Judith, R.I., as part of a study of the Southern New England industrial fishery. These data (sexes combined) were used to calculate the length-weight relation presented in table 3.

TABLE 3.—*Length-weight relation for spiny dogfish, sexes combined, Point Judith, R.I., October 1955*

Length	Weight	Length	Weight
Cm.	*G.*	*Cm.*	*G.*
28	75	64	920
31	90	67	1,050
34	110	70	1,200
37	140	73	1,370
40	180	76	1,550
43	230	79	1,780
46	310	82	2,000
49	390	85	2,250
52	470	88	2,560
55	570	91	2,850
58	680	94	3,200
61	790		

POPULATION STATUS

The total population of the spiny dogfish is not known, although there is no doubt that it is relatively abundant and may be subject to long-term fluctuations in abundance. In the spring of 1846 they were so numerous around Gay Head, Mass., that 600 were caught on hooks in 1 day by the crew of a single boat (Storer, 1867).

Collins (1884) relates an eyewitness report from a fisherman who observed a school of mackerel at the surface of Wood Island, Maine, that was being harried by an immense school of dogfish in August 1880. The fisherman estimated there were about "100 barrels of dogfish" in the school. The dogfish surrounded the mackerel ". . . in such a manner as to inclose the mackerel on all sides and underneath, completely preventing their escape." Many of the mackerel were seen with their tails bitten off and with wounds in their flanks.

Cod as well as mackerel suffered from the attacks of the dogfish. Earll (1880) considered the dogfish to be the principal enemy of the cod and reported that adult cod in the market were seen to have teeth marks and spine wounds in their flesh, a result of attacks by dogfish. "The arrival of a school of dogfish in any locality," Earll noted, "is the signal for all other species to leave; and in this way the work of the fisherman is often suddenly terminated."

Bowers (1906) reported good groundfishing in Boston Bay in July and August 1903, but in 1904 ". . . horned dogfish [were] present in such great numbers that it was impossible to catch anything else."

Dogfish were much more numerous in Massachusetts Bay during the last quarter of the 19th Century and during the early 1900's than they had been previously, although in the Woods Hole region they were more plentiful before 1887 than they have been at any time since (Bigelow and Schroeder, 1953). These authors felt that perhaps the period 1904–05 marked a peak in the cycle of dogfish abundance.

It may be, however, that the population of dogfish does not fluctuate greatly but that in their seasonal migrations the main body of fish may visit one area this year and other areas next year. Our lack of knowledge about the nature of the population(s) makes it difficult to come to any firm conclusion regarding the absolute or relative numbers of fish involved.

As a result of his early studies of the dogfish around Newfoundland, Templeman (1944) said, "It is obvious . . . that dogfish migrate rapidly and for long distances, and since they swim chiefly in the upper layers of water there are no hinder-

ances to migration such as the contours of the bottom offer to haddock and cod. Thus, it is quite possible that the dogfish stocks on the whole eastern coast of North American mingle sufficiently to constitute a single population."

He modified this somewhat later (1954) after analyzing his tag return data. "The distant recaptures are also numerous enough, considering the small number tagged, and occur in enough different years to show that even if there is not indeed a single population, there is at least a widespread intermingling of the populations of adult female *Squalus acanthias* on the Atlantic Coast of North America."

Exploratory cruise data indicate that, rather than being distributed relatively homogeneously over large areas, dogfish congregate in dense, localized schools. Thus, high concentrations of dogfish at a given time and locality provide no accurate indication of their overall abundance, as they may be exceedingly scarce a few miles distant. Large hauls of dogfish tend to be grouped within a period of a few days, as the vessel fishes the same general area during the interval. Similarly, consecutive tows at different depths may produce no dogfish at one depth but numerous dogfish at only slightly greater depths (table 4).

There is evidence that dogfish may vary in availability, or abundance, from year to year as well as from place to place. Data were analyzed from survey cruises of the research vessels *Albatross III* and *Delaware* (table 5). The relative abundance of dogfish, expressed as catch per 30-minute tow, was high in 1948, 1949, and 1950. Abundance declined markedly in 1955 and 1956 but was moderately high in 1958. In 1959, abundance of spiny dogfish declined once more, but during 1960–62 it reached a high level nearly on a par with the peak in 1949. The changes in abundance are also reflected in the commercial catch of dogfish (see figs. 8 and 9). No explanation exists for this apparent periodicity in abundance.

TABLE 4.—*Dogfish catches on* Albatross III *Cruise 126, by depth, temperature, and sex along Middle Atlantic Coast, January–February 1959*

Transect	Date	Depth	Bottom temperature	Males	Females	Total fish
		Meters	*° C.*	*Number*	*Number*	*Number*
Martha's Vineyard	Feb. 3	85	5.6	48	11	59
		116	11.7			
		150	10.6	14	353	367
		183	9.4	423	5	428
		268	8.9			
		384		2		2
Hudson Canyon	Feb. 2	58	7.2	10		10
		85	8.9	40	2	42
		122	11.1	5	5	10
		168	10.0			
		186	9.4			
		326	6.7			
		417				
Barnegat	Jan. 23	46	7.2			
		82	10.6			
		113	11.1			
		146	11.1			
		289				
Cape May	Feb. 1	58	10.0	53	4	57
		79	11.7	144	138	282
		113	11.7	251	466	717
		158	11.1			
		213	10.0			
		280				
		329				
Delaware Bay	Jan. 24	55	10.0	14		14
		76	12.2	53	66	119
		119	12.2	2	1	3
		146	11.1	1	1	2
		184	11.1			
		229	9.4			
		274				
		402				
Winterquarter	Jan. 25	33	10.0	58	1	59
		67	12.2	4	1	5
		70	13.3	1		1
		131	11.1	17	8	25
		238				
		436				
Cape Charles	Jan. 25	31	8.9			
		43	12.2	25	56	81
		76	12.8			
		141	12.2			
		196	10.0			
		317				

TABLE 5.—*Spiny dogfish catch on annual survey cruises, all seasons, all grounds from Nova Scotia to Hudson Canyon, 1948–62*

Year	Total tows	Tows with dogfish	Total caught	Catch per tow
	Number	*Number*	*Number*	*Number*
1948	233	57	4,551	19
1949	115	21	3,755	33
1950	339	173	10,333	31
1955	279	64	672	2+
1956	93	40	727	8
1958	159	63	1,923	12
1959	212	38	1,106	5+
1960	117	41	2,636	22
1961	161	42	3,799	23
1962	138	37	3,444	25

POPULATION DYNAMICS

The dynamics of the spiny dogfish population would be difficult to study now to any fine degree because much of the necessary information is lacking or is imperfectly known. Perhaps the greatest gap in our understanding of the species is a knowledge of the nature of the population itself.

The basic plus and minus factors of natality and mortality lack adequate quantitative investigation. There have been some studies, however, of certain phases in the reproductive cycle, and these are discussed below.

REPRODUCTION

Spiny dogfish are ovoviviparous. The eggs in the female are fertilized internally by means of the

male's claspers, and the young are born alive. The period of fetal development is lengthy, perhaps up to 2 years. The number of young produced at each delivery by a female dogfish is small.

Sex Ratio

During development in the females, and presumably at birth, the sex ratio of the pups is very nearly 1:1. Ford (1921) collected 2,720 embryos at the fish market in Plymouth, England, and found 1,377 were males and 1,343 were females. Templeman (1944) counted 933 males and 931 female embryos in the uteri of 492 females collected in July–November 1942, off St. John's, Newfoundland. For dogfish in the Pacific, Bonham et al. (1949) report, "Males and females occur in equal numbers among the embryos." Aasen (1964b) examined the pups in a sample of 41 females collected in November 1958 about 100 miles west of the Orkney Islands. There were 126 males and 130 females. Our observations for dogfish in the Gulf of Maine agree with those from other waters. In July–August 1961 on a cruise of the *Delaware* in Ipswich Bay, 234 female dogfish were examined. Fifty-three contained pups, of which 155 were males and 140 were females.

From the time of birth to the time of attaining sexual maturity, the young dogfish tend to school together, but the mature adults tend to school by sex. Ford (1921) classified the schools, or shoals, as follows: (1) Shoals of large fish consisting exclusively of females, the majority in the pregnant condition; (2) shoals of medium-sized fish exclusively males in the mature condition; (3) shoals of medium-sized fish of which the majority were immature females; and (4) shoals of immature fish in which the males and females were equal in number.

Sex-size segregated schools are also reported by Hickling (1930) around Ireland, Templeman (1944) off Newfoundland, and Bigelow and Schroeder (1953) in the Gulf of Maine. In the eastern Pacific, however, Quigley (1928b) observed that the schools contained both sexes, and the data listed by Bonham (1954) for the same general area support this statement, although in individual catches the percentage of males varied as much as from 35 to 76 percent. In the western Pacific, however, Kaganovskaia (1933) observed the schools of dogfish to be segregated by sex, size, age, and depth. She notes, ". . . the shore-set nets caught mainly immature sharks from 4 to 8 years of age, the bottom-set nets older fish, from 10 to 18 years, mainly males—(July–October); the drift pelagic nets—chiefly mature females." Thus, her observations agree in general with those reported from other parts of the world. I suspect that the dogfish in the eastern Pacific also school by sex despite the reports to the contrary by Quigley (1928b) and the data presented by Bonham (1954).

On the basis of the reports from areas that include the known range of the spiny dogfish, it is difficult, therefore, to determine the sex ratio of the adults because of the manner in which they school.

Size at Sexual Maturity

Sexual maturity in male dogfish is attained at a smaller size than in females, and reported studies indicate that the larger the maximum size of fish in a population, the larger the size at maturity. Table 6 lists the data extracted from reports that specifically mention average size at first maturity for the spiny dogfish.

TABLE 6.—*Maximum size and size at first maturity of spiny dogfish from several areas*

Author	Locality	Size of males		Size of females	
		Maturity	Maximum	Maturity	Maximum
		Cm.	*Cm.*	*Cm.*	*Cm.*
Ford (1921)	Plymouth, England.	59–60	83	70–80	110
Hickling (1930)	Irish Sea	62		70–80	
Kaganovskaia (1937).	Sakhalin			100	[1] 124
Templeman (1944)	Newfoundland	60	86	74	101
Bonham et al. (1949)	Washington	72	100	92	124

[1] Sex not specified, probably a female.

Because of the age determination problem discussed earlier, it is difficult to assign an age value to the time of first maturity. Templeman (1944), however, suggests that, ". . . it takes the average female dogfish 9 or 10 years from the fertilized egg or 7 or 8 years after birth to reach sexual maturity." Based on the spine readings of Bonham et al. (1949), the data indicate 11 years for males and 19 to 20 years for females as the age of first maturity for spiny dogfish in waters off Washington. Kaganovskaia (1937) did not discover mature females less than 19 years old or less than 1,000 mm. long. It seems incredible that dogfish mature at such a late age, but a critical examination of the evidence offers support for Bonham's data and Kaganovskaia's statement.

The reported sizes of spiny dogfish at time of first maturity are about 72 percent (range 68–80 percent) of the reported maximum sizes for the species. This is in general agreement with similar data reported by Bigelow and Schroeder (1953) for nine species of sharks from the Gulf of Maine where the sizes at first maturity are about 62 percent (range 52–75 percent) of the maximum sizes. If we assume (1) that the maximum age (sexes combined) of the spiny dogfish is 25 to 30 years, (2) that we can equate length with age, and (3) that the largest individuals are females, then the age at first maturity of the females is about 72 percent of the maximum or about 18 to 21 years.

Mating

Although there are no recorded observations of the actual mating of spiny dogfish and no conclusive data to confirm the season of year when it takes place, the evidence presented by most authorities suggests that mating takes place during months when the water temperatures are low. Ford (1921) found newly formed embryos at Plymouth during November to May. Templeman (1944) concludes that the eggs are fertilized and pass into the uteri in February and March, but more generally in March. He cautions, however, that his lack of information about the spring temperatures when the eggs are developing may vary the dates a month in either direction. An examination of dogfish captured in the Woods Hole area suggests that ovulation probably occurs in February or March (Hisaw and Albert, 1947) and perhaps we can infer that mating and fertilization of the eggs take place soon after. Bigelow and Schroeder (1948) believe that in the Atlantic Ocean, mating probably takes place shortly after the young are born, although no definite information is available.

Reports on mating of the spiny dogfish in the Pacific Ocean tend to be contradictory, but in general support the hypothesis that mating takes place in the cold months, as in the Atlantic Ocean. Quigley (1928b) examined slightly over 200 dogfish collected in June, July, and August and found embryos that ranged in size from the smallest to those with the umbilical scar completely healed and apparently ready for birth. These observations suggested that ". . . in the vicinity of Nanaimo, *Squalus sucklii* breeds at all times of the year." We know now, of course, that what she had seen were the two broods of young that are typical of the species. Hart (1942) on the other hand, reporting the work of Lucus, concluded that breeding takes place during the winter and that, ". . . fertilization by the male takes place soon after the birth of the young . . ." Bonham et al. (1949) admitted that the season at which mature dogfish mate is not known, but regards as a popular misconception the belief that dogfish breed and bear young at all times of the year. Sato (1935) concluded, without much firm basis for the statement, that dogfish breed throughout the year around Hokkaido.

Fecundity

As might be expected for a live-bearer, the number of young produced per female spiny dogfish is small and the period of development within the mother is long, lasting nearly 2 years. The eggs are large and contain a great deal of yolk and have been well described by Templeman (1944). Following fertilization, and during early development of the fetus, the eggs (figs. 6 and 7) are contained in a horny capsule ("candle") that later breaks down leaving the embryos free in the enlarged part of the oviduct (termed the "uterus"). There is no placental attachment (Bigelow and Schroeder, 1953) as with some other species of sharks, but additional material (at least water) is obtained from the uterine wall (Templeman, 1944). The reported number of pups per female probably should be considered a minimal figure. The observations were made of fish caught by otter trawls or other fishing gear and examined on board the vessel or in the market. I have seen pups that were apparently near term prematurely delivered when the females were landed on the deck of our research vessel. It seems reasonable to assume that this also happened in the studies reported in the literature. Fortunately, the number of premature pups was never very great so that the reported data may be accepted with a fair degree of confidence.

The greatest number of pups per female was reported by Kaganovskaia (1937) who recorded 5 to 19, with an average of 11, for the spiny dogfish near Sakhalin. The least number of pups per female was reported by Templeman (1944) who recorded 1 to 7, with an average of 4, for the dogfish near Newfoundland. Ford (1921) reported 1 to 11, mostly 2 to 4, from England, while from the

795–358 O—66——2

FIGURE 6.—Spiny dogfish egg collected July 1961 in Ipswich Bay. Note the embryo, probably about 4 months old.

West Coast of North America, Quigley (1928b) reported 3 to 11 (average 7), Clemens and Wilby (1961) reported 3 to 14, and Bonham et al. (1949) reported 2 to 17, mostly 7 to 8. Female spiny dogfish collected about 100 miles west of the Orkney Islands contained 2 to 13 pups, with an average of 6.2 pups per female (Aasen, 1964b).

In the Gulf of Maine, Bigelow and Schroeder (1953) state that the number of pups per female may be as many as 8 to 11, or as few as 2, but mostly 4 to 6. Data collected in July–August 1961, in the inner Gulf of Maine (Ipswich Bay), show the females may contain from 1 to 11 pups, mostly 4 to 7.

To examine the relation between the size of pregnant female and the size and number of pups (fetuses) per female, I grouped the data by length of females by 3-cm. groups (table 7). In addition to the data for fetuses, the measurements and numbers of embryos are also included.

TABLE 7.—*Fecundity of spiny dogfish examined aboard R/V* Delaware, *1961*

Length	Females with embryos	Embryos		Females with fetuses	Fetuses	
		Average per female	Average length		Average per female	Average length
Cm.	*Number*	*Number*	*Mm.*	*Number*	*Number*	*Mm.*
60	1	5.0	4			
63						
66						
69						
72						
75	1	5.0	5			
78	1	3.0	5	2	4.5	154
81				2	6.0	190
84	2	4.5	3	6	4.7	186
87	6	4.5	9	6	3.7	194
90	4	4.2	12	14	5.6	197
93	4	6.2	7	9	5.6	194
96	1	9.0	6	5	7.2	197
99				8	7.9	205
102	1	3.0	20	1	8.0	220

The data suggest that the larger females tend to have slightly more and slightly larger pups than the smaller females. This, in general, agrees with the reports from other parts of the range of the spiny dogfish. A comparison between the aver-

FIGURE 7.—Microphotograph of the embryo shown in Figure 6. Actual size of embryo is 19 mm.

age number of embryos per female and the average number of fetuses per female seems to indicate there is very little loss (mortality?) between the two stages of development. The size of the young dogfish at the time of birth is 20–30 cm., regardless of the part of the world from which the observations are reported (table 8).

TABLE 8.—*Size of dogfish at birth*

Author	Locality	Reported size of dogfish pups
		Cm.
Ford (1921)	Plymouth, England	25–31.
Hickling (1930)	Irish Sea	About 26.
Kaganovskaia (1933, 1937)	Sakhalin	Average 24.
Templeman (1944)	Newfoundland	24–31.
Hisaw and Albert (1947)	Woods Hole, Mass.	25–30.
Bigelow and Schroeder (1948)	Gulf of Maine	22–33.
Bonham, et al. (1949)	State of Washington	Average 27.
Aasen (1964b)	Orkney Islands	Average 26.

Process of Birth

There are two recent instances of spiny dogfish giving birth to young in tanks at the Bureau's Woods Hole aquarium. In one instance, I suspect the female aborted rather than having a normal, full-term delivery.

The first dogfish was caught with hook and line October 19, 1962, in water about 27 m. deep. The surface water temperature was 14.2° C. The fish was placed in the aquarium the same day, in water of the same temperature, and apparently adjusted well to the tank conditions. On November 22, 1962, during the night, she gave birth to three pups that measured 20.0, 20.3, and 20.7 cm. None of the pups had any evidence of the yolk sac except for a small scar on the ventral surface between the pectoral fins where the yolk sac had been attached. Presumably the yolk had been resorbed and the pups were fully developed. The water temperature in the tank at the time was 8.4° C. The pups did not survive, although the mother continued to live for several weeks until she was sacrificed.

The second dogfish was collected in a fish trap and placed in the aquarium on July 24, 1963. The next day the aquarium attendant observed the delivery of two pups. The female was resting motionless at a slight incline on a pile of rocks in the tank. Two pups were delivered simultaneously, head first, in rhythmical movements that suggested uterine contractions during mammalian birth. Delivery of the two pups took about 10 minutes. The female also delivered four more pups, but the aquarium attendant had been called

away and could not observe the delivery. An hour later, about 2 cm. of the caudal fin of a pup could be seen protruding from the female's vent. This pup was not delivered, and the female died later in the day. The average length of the pups was 21 cm., and each had a yolk sac attached. Although their size suggests the pups were nearly full term, presence of the yolk sac indicates they were still developing. Presumably the female aborted, perhaps from the shock of capture and handling or perhaps from the water temperature. The surface water temperature in the trap was 19.5° C. and the tank temperature was the same. This is well above the temperature where the species is commonly found.

When the female was examined, post mortem, the partially delivered pup was found to be held by one dorsal spine in the anterior part of the female's left uterus. The dogfish pup is morphologically suited to head presentation in birth. No doubt the caudal presentation noted here was accidental; the rearward sloping dorsal spines—small as they are—deter smooth, tail-first movement out of the uterus. It is not known if partial delivery occurs among dogfish in the sea, and none has been observed aboard our research vessels.

Season of Birth

The gestation period of dogfish is nearly 2 years, although the authorities differ in the exact number of months involved. Birth generally occurs in the cold months of the year. Ford's (1921) extensive studies at Plymouth led him to conclude that gestation occupies 21–25 months, with the fetuses ready for birth from August to December. Hickling (1930) confirmed Ford's findings. Templeman (1944) suggested a gestation period of almost 24 months with birth between January and May. Assen's (1964b) data suggest that in the offing of the Orkney Islands, dogfish pups are ready for birth in late November or soon after.

A somewhat shorter gestation period for dogfish captured in the vicinity of Woods Hole is reported by Hisaw and Albert (1947) who state, "The gestation period apparently covers about 20 to 22 months and a female gives birth every other year." The pups, they note, are born in the late fall, somewhere south of Woods Hole. Bigelow and Schroeder (1953) report a gestation period of 18 to 22 months with birth probably taking place on the offshore wintering grounds, although some may be born in the spring and summer. Latham (1921) confirmed that some may be born in the summer when he reported many young dogfish only a few hours old that were caught in a fish trap in Long Island Sound in August.

In the Pacific the gestation period is 2 years with birth taking place during the winter (Hart, 1942), more specifically in November and December (Bonham et al., 1949).

An individual female produces young only in alternate years (Hart, 1942; Hisaw and Albert, 1947; Bonham et al., 1949; Clemens and Wilby, 1961). The data presented by Ford (1921), Hickling (1930), and Templeman (1944) confirm the broods-in-alternate-years conclusions of the workers cited above.

MORTALITY

The spiny dogfish has few enemies and is cannibalistic only to a very small degree. Thus, except for disease, there is little to act as a deterrent to the buildup of dogfish populations, and this no doubt is one of the prime reasons for the vast numbers of dogfish reported in one area or another. The predators of the spiny dogfish are mostly the large sharks and large bony fishes. In table 9, I have listed the predators as reported in Bigelow and Schroeder (1953) and noted certain appropriate remarks. It should be stressed that in all but two of the instances the prey is specifically identified as the spiny dogfish. The remaining two instances were simply listed as "dogfish" and possibly may be the smooth dogfish.

TABLE 9.—*Predators of the spiny dogfish*

Predator	Remarks
Mackerel shark (*Lamna nasus*)	Known to prey on spiny dogfish in the eastern Atlantic; probably Gulf of Maine also.
Maneater (*Carcharodon carcharias*)	One spiny dogfish, evidently torn off a line trawl.
Tiger shark (*Galeocerdo cuvier*)	Dogfish (species ?) from one captured in Woods Hole.
Blue shark (*Prionace glauca*)	Preys on spiny dogfish in northern waters.
Barndoor skate (*Raja laevis*)	Spiny dogfish from Woods Hole records.
Lancetfish (*Alepisaurus ferox*)	Small spiny dogfish eaten by Block Island specimen.
Tuna (*Thunnus thynnus*)	Swallowed whole dogfish (species ?) weighing 8 pounds.
Tilefish (*Lopholatilus chamaeleonticeps*)	One contained two spiny dogfish.
Goosefish (*Lophius americanus*)	One contained a spiny dogfish 1 foot long and the vertebral columns of 6 others.

Marine mammals apparently are not a threat to the dogfish. In a study of the food habits of seals (Fisher and Mackenzie, 1955), dogfish remains

were found in the stomach of a grey seal (*Halichoerus grypus*) but constituted only 1 percent of the volume of the stomach contents. Killer whales (*Grampus orca*) may feed on dogfish, but probably only when other food is unavailable. One killer whale was seen, "Scavenging round longlining vessel, eating dogfish." in the Strait of Belle Isle, July 1953 (Sergeant and Fisher, 1957). No doubt the relatively large size, spines, and tough, scabrous skin of the dogfish are effective deterrents to predation.

UTILIZATION OF THE SPINY DOGFISH

The dogfish is not completely valueless or useless. It has some slight value, in limited quantity, in the United States, and it has greater value in some parts of the world where it is sought as a food fish. The greatest value of the dogfish in North American waters is as an industrial fish for processing into oil and meal, and at one time it was under intense exploitation for its liver as a source of natural vitamin A (fig. 8).

The Bureau of Commerical Fisheries collects and publishes yearly summaries [3] of U.S. fisheries by regions. In this paper, data collected from the Puget Sound, Middle Atlantic, and New England regions are discussed. The data given in table 10, and shown in figures 8 and 9, are taken from various sections of the statistical reports.

TABLE 10.—*Catch of grayfish* [1] *at principal regions, 1915–61*

Year	New England States		Middle Atlantic States		Puget Sound, Wash.	
	Catch	Value	Catch	Value	Catch	Value
	Pounds	*Dollars*	*Pounds*	*Dollars*	*Pounds*	*Dollars*
1915					7,093,996	15,959
1919	63,667	184				
1922					6,359	22
1923					53,400	70
1924	21,950	367			97,005	247
1925					41,549	86
1926			6,755	347	290,395	1,452
1927					89,707	449
1928	206,309	3,312			3,203	16
1929	213,306	2,829	38,605	552	286,419	1,060
1930	93,196	3,049	12,690	267	371,180	1,309
1931	44,330	454	4,796	90	778,560	2,335
1932	27,049	374	8,140	81		
1933	13,428	151	6,739	135		
1934						
1935	35,300	733	115,500	2,053	277,500	527
1936					330,700	764
1937	31,600	578	57,700	545	1,620,100	14,360
1938	46,200	1,111	102,200	1,021	578,100	4,153
1939	85,700	1,124	47,800	478	2,365,200	17,738
1940	575,500	19,426	51,800	1,009	3,341,100	36,504
1941 [2]	575,500	19,426	51,800	1,009	23,532,300	751,620

See footnotes at end of table.

TABLE 10.—*Catch of grayfish* [1] *at principal regions, 1915–61*—Continued

Year	New England States		Middle Atlantic States		Puget Sound, Wash.	
	Catch	Value	Catch	Value	Catch	Value
	Pounds	*Dollars*	*Pounds*	*Dollars*	*Pounds*	*Dollars*
1942			127,300	3,802	16,932,400	668,863
1943	89,700	1,637	47,300	1,959	22,021,500	1,243,858
1944	53,300	1,446	6,600	200	39,513,700	2,094,217
1945	31,100	565	31,000	1,211	22,149,100	1,063,149
1946	107,600	2,472	54,200	3,327	20,991,800	1,366,513
1947	24,000	455	21,200	1,046	14,984,800	954,535
1948	55,100	775	3,000	150	12,302,700	711,125
1949	625,200	5,718	55,500	2,163	10,587,000	447,828
1950	111,200	1,171	37,200	1,829	1,914,600	33,197
1951	39,600	539	63,700	3,051	2,412,900	58,750
1952	11,200	254	42,700	1,857	2,981,400	47,535
1953	9,000	<500	65,000	3,000	2,225,600	17,669
1954	2,000	<500	61,000	3,000	2,008,800	19,931
1955	7,000	<500	86,000	3,000	1,935,300	14,029
1956	486,000	4,000	60,000	2,000	1,526,400	12,808
1957	1,287,000	10,000	55,000	2,000	1,860,900	33,390
1958	893,000	8,000	50,000	1,000	4,233,100	26,675
1959	763,000	6,000	71,000	3,000	3,091,900	28,189
1960	1,006,000	7,000	52,000	2,000	1,378,400	6,931
1961	970,000	6,000	70,000	3,000	790,700	3,953

[1] Grayfish is the market name for dogfish.
[2] No survey on east coast. Data reported were those collected in 1940.

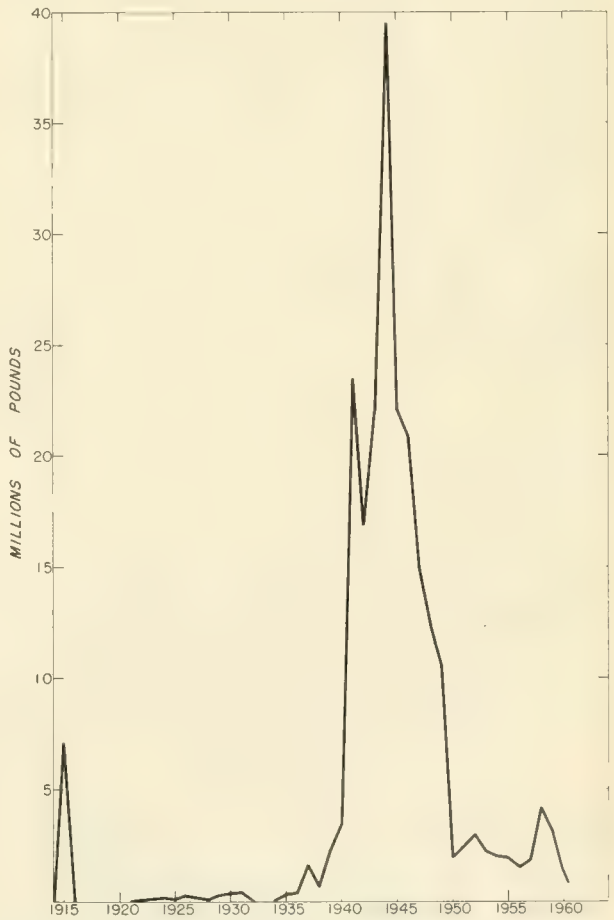

FIGURE 8.—Dogfish catch from Puget Sound, Wash., 1915–61.

[3] Fishery statistics of the United States, 1919–63, U.S. Department of the Interior, Fish and Wildlife Service, and predecessor agencies.

The fishery for dogfish on the west coast of the United States has been studied by Alverson and Stansby (1963), who discussed the technological developments in the use of dogfish and some methods for control of the extensive populations. They reviewed the fishery and its effects on the abundance of the dogfish and recommended that an economic use be developed for the dogfish and that research be instituted to determine the biological effects of control of the species.

The possible uses of dogfish are the subject of an extensive review by Osterhaug (1961), who included a bibliography of 166 references on the subject. The first part of the review discusses the significance of the urea content of dogfish flesh. The second part discusses possible uses including animal feeds, particularly for ruminants that are able to utilize urea in their diets.

The fishery for dogfish on the east coast of the United States was never as intensive, nor did it ever reach the heights reported for the fishery on the west coast. However, from time to time the east coast fishery was active for oil, guano, meal, and human food (fig. 9). Details of the fishery are outlined below.

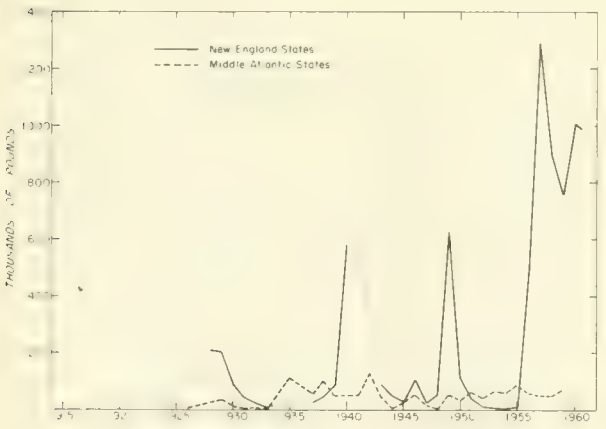

FIGURE 9.—Dogfish catch from the New England and Middle Atlantic States, 1919–61.

INDUSTRIAL USES

One of the earliest mentions of an industrial use for dogfish was made by Perley (1852), who reported on the species in the Gulf of St. Lawrence. He noted that the skins were used by cabinet makers to polish hardwood, the livers were used for oil, and the carcasses were dried and fed as a winter food supplement to cattle. Pigs in particular were said to thrive on this diet.

Reduction for Oil and Meal

A fishery for dogfish existed around Provincetown, Mass., during the late 19th century and was prosecuted with handlines baited with silver hake (Storer, 1867). The fishery took place in September through November when the dogfish appeared in the area during their seasonal migration. Only the livers were wanted for their oil—one thousand livers yielded one barrel of oil—and the oil was sold to tanners and curriers for preparing and treating leather.

In other places, the whole dogfish was used for reduction, especially when more desirable species such as menhaden were less abundant. A menhaden reduction plant in East Boothbay, Maine, processed dogfish for oil and guano (Gallup, 1883). The fishermen were paid $1 per 100 fish, but it was suggested that the Federal government pay a subsidy to encourage greater fishing effort. Spiny dogfish was the principal species used for oil and guano when a guano factory was established at Woods Hole (Smith, 1898), but a scarcity of the species in the season of 1897, and the general irregularity of their supply, caused the factory to turn to menhaden for raw material.

Many early writers tried to stimulate utilization of the dogfish by citing the different ways the fish could be used. I. Field (1907) mentions that dogfish oil (liver oil?) was used for illumination in some areas and that on Cape Cod the carcasses were dried and used for fuel. G. Field (1912) reports that on Cape Breton Island dogfish were dried on fences and fed to horses as a diet supplement and the well-yolked eggs were used experimentally as a substitute for hen's eggs to tan leather.

Barraclough (1953) cites interesting historical information about the early uses and developments of dogfish oils in and around the coastal areas of British Columbia. The local Indians processed the livers and used the oil obtained for dressing skins and hides. Later, as lumbering operations began in the area, the oils were used to lubricate skidways on logging roads. The oil was used extensively for lubrication and illumination in sawmills, coal mines, and coastal lighthouses. Most of the oil was processed in small home-type operations, but in 1877 the first large commercial

factory was established for oil production. It is worth noting here that during the time of World War I (1916–18) almost the entire catch of dogfish from British Columbia was exported as "grayfish" to the U.S. fresh fish market.

Extraction of Vitamin A

No doubt the greatest industrial use of the dogfish took place about 1937–47 when the species was fished intensively in Puget Sound and surrounding waters. Their rich, oily livers were in demand as a valuable source of natural vitamin A. The livers contain 50–75 percent oil, and the vitamin A content of the oil is 5,000 to 30,000 U.S. Pharmacopeia (U.S.P.) units per gram (Harrison and Samson, 1942).

The first extraction of vitamin A from shark liver oil was begun on a commercial scale about 1936–37, and the dogfish fishery was underway in Puget Sound in 1937–38 (Harrison and Samson, 1942). The fishery was on a small scale until about 1940, then, with the entry of the United States in World War II and the loss of foreign sources of vitamin A from cod liver oil, the fishery increased in intensity. In 1940 the average price paid to the fishermen for the livers was 5.7 cents per pound, but by 1943 the average price was 46 cents per pound and at one point reached a high of 54 cents (Bonham et al., 1949). The intensity of the fishery undoubtedly had a marked effect on the size of the dogfish population. Barraclough (1953) reports a decline in availability of the species in Hecate Strait beginning in 1944.

Dogfish liver oil has high vitamin A potency. Bonham et al. (1949) note that oil rendered commercially from livers of dogfish taken in the waters in and around Washington varies from 5,000 to 25,000 U.S.P. units of vitamin A per gram. The vitamin values increase several hundred percent when the fish attain sexual maturity, and the content is greater in winter than in other seasons. In contrast, Templeman's (1944) laboratory extractions of vitamin A from Canadian dogfish liver oil ranged from 300 to 19,700 U.S.P. units per gram with an average value for immature females of 1,183 units, for mature males of 1,662 units, and for mature females of 2,780 units. (For purposes of comparison, pharmaceutical cod liver oil must contain not less than 850 U.S.P. units of vitamin A per gram (Bailey, 1952).) Hirao, Yamada, and Kikuchi (1959) report vitamin A values of spiny dogfish flesh from 329 to 5,220 U.S.P. units per 100 grams of flesh. Liver oil from the same fish contained from 2,080 to 38,800 U.S.P. units of vitamin A per gram.

Following the end of World War II, two major events occurred that had a devastating effect on the west coast fishery for dogfish. First, foreign sources of vitamin-rich fish oils again became available, and second, vitamin A was synthesized in 1947. Soon after this the dogfish fishery collapsed except for relatively small volumes landed for reduction and an extremely limited food market.

During World War II the Canadian government became interested in the east coast dogfish liver oils and their vitamin content, but the prices paid to the fishermen were too low to develop a fishery (Templeman, 1944).

Oils obtained from dogfish are of value today chiefly as raw materials for other industrial processes. The liver oil is sulfurized and used as a rubber extender, and the body oils are used in the tanning of leather (Bailey, 1952).

New England Industrial Fishery

The late 1940's saw the beginning of a new kind of fishery in New England—the so-called trash or industrial fishery—in which nonfood species, including spiny dogfish, were landed in great quantities for reduction to meal and oil. Sayles (1951) marks 1948 as the start of the trash fishery at southern New England ports with the processed meal destined for use as supplements in hog and poultry feeds.

The amount of dogfish used was small at the start of the industry. For example, the species composition of a sample from one boat that landed at New Bedford in October 1949 included only 1 dogfish in the sample of 536 fishes (Snow, 1950), but by 1956, 259,000 pounds of spiny dogfish were landed by the industrial fleet at New Bedford (Edwards and Lux, 1958). The dogfish represented 1 percent of the total industrial landings and were caught off No Mans Land, mostly in November and December.

In 1957 the Southern New England industrial landings of spiny dogfish were slightly more than 5 million pounds (3 percent of the total), with most of them landed at Point Judith, R.I. (Edwards, 1958a). There were two peaks in the landings of dogfish, one in the spring and one in

the fall, no doubt representing periods when they were locally abundant during their migrations. The industrial fishery fleet at Gloucester caught quantities of dogfish off Cape Ann, Mass., on Stellwagen Bank, and off Nauset, Mass., although the volume landed represented only from 1.5 to 3 percent of the total pounds landed (Edwards, 1958b).

Reduction plants do not like to process large amounts of spiny dogfish because they yield only meal, with very little oil, and there are serious mechanical problems involved in handling the species. The rough skin of the dogfish causes these fish to jam conveyor belts, and to pack in bins and chutes. The collagen in the carcasses clogs screens (Tarr, 1958). Tarr also states that the dogfish result in a poor yield of meal compared to other fishes.

Change in the design of processing machinery is suggested as one way to overcome the problems in handling dogfish carcasses. For example, installation of grinders designed specifically for dogfish may solve the jamming problem, but further technological research is needed before dogfish carcasses can profitably be used (Alverson and Stansby, 1963).

The rapidly expanding pet-food industry has been suggested as a potential user of great quantities of dogfish. Jones (1959) reports that on the Pacific coast the estimated potential annual production of dogfish for dog and cat food is on the order of 60 to 80 million pounds.

FOOD USES

A vast protein food resource is wasted each year in the United States because only infinitely small amounts of spiny dogfish are used for human food. Under present economic conditions, however, and because of prejudice toward eating shark flesh, it probably would be most unprofitable to fish and market dogfish for human food.

The repugnance (and perhaps fear) that most people feel towards sharks in particular does not help to make dogfish popular as a food fish. The very name "dogfish" connotes something not suitable for humans. Efforts to disguise the species under a euphemism have included simply not mentioning what it was. Thus, Field (1907) reports it was served as "fish" on two occasions in the Marine Biological Laboratory (Woods Hole) mess hall and enthusiastically accepted by the unsuspecting diners. It has been served experimentally in hotels and listed on the menu as "Japanese halibut." In England, dogfish are gutted, skinned, beheaded, and marketed as "flake" and "rock salmon" and are widely used as one of the ingredients in the popular carryout dish, fish-and-chips.

In the United States during World War I, a great effort was made to popularize a number of relatively unexploited fishes to increase their acceptance by the consumer and thus relieve the war-induced meat shortage. Spiny dogfish was one such fish, and it was dubbed "grayfish," the name by which it is marketed today. A 14-ounce can of grayfish sold retail for 10 cents, and a Government circular (U.S. Bureau of Fisheries, 1916) was published in which 17 different recipes for preparing grayfish were listed.

Canned grayfish did not prove to be a practical solution to the problem of dogfish utilization. Corrosion of the cans, caused by changes in the chemistry of the meat, and the offensive ammonia smell that developed caused the buying public to reject the product. The flesh of dogfish, as with other elasmobranchs, contains large amounts of urea, which rapidly decomposes to form ammonia (Mavor, 1921). Fresh and frozen dogfish tissue contain about the same amounts of urea (0.9–1.5 percent), and hydrolysis, with the subsequent release of ammonia, occurs in the frozen flesh (Benson, 1924). Moyer, Southcott, Baker, and Tarr (1959) tested several methods of storing fresh dogfish flesh for periods up to 21 days. The storage included in ice and in refrigerated sea water, with and without added antibiotics (chlorotetracycline). They concluded, ". . . dogfish, when stored under nearly ideal conditions, appear to spoil no more rapidly than most other sea fish." It seems obvious though that dogfish is best eaten when very fresh.

The keeping quality of dressed dogfish was further studied by Southcott, Moyer, Baker, and Tarr (1960). The fish were stored in individual polyethylene bags at 0°, 5°, and 10° C., with a control lot unbagged in crushed ice. The experiment lasted 21 days. Each day two fillets were cut from a single fish from each treatment and used for bacteriological and chemical determinations. The authors found that, "Less ammonia and

trimethylamine were produced in iced fish samples than in bagged fish samples at 0° C., although bacterial counts in the two treatments were comparable." They suspected, however, that the melt water from the ice leached some of the chemical products from the flesh. Bacterial and chemical values rose rapidly at 5° C. and 10° C., and these treatments were ended at 17 days and 8 days, respectively. In general, pronounced ammonia odors were noted in only a few samples, and these were "strongly masked" by putrid odors.

Dogfish flesh is quite palatable and may be prepared in a variety of ways. My family and I have eaten fried dogfish fillets and enjoyed the meal. The fillets are easily cut from the fish and easily skinned. The meat is bone-free and white and has a flaky consistency and firmness similar to haddock fillets. The flavor is mild, and the frying produced no odors other than would be expected with any fish.

Dogfish fillets were prepared in several different ways and eaten by a test panel at the University of Washington in 1959 (Liston, 1960). The steamed fillets were rated very good and brined and smoked dogfish was well accepted. In a comparison between fishsticks made with dogfish and two brands of fishsticks bought in a retail store, those made with dogfish were rated as first or second preference by all panel members.

Dogfish is popular in Europe today as a food fish, not only in England but also in Continental Europe. In 1960, 25,600 metric tons, worth nearly 11 million kroner (1 krone is about (U.S.) 14 cents), were landed by Norwegian fishermen and shipped to England (Food and Agriculture Organization of the United Nations, 1961). It is marketed both in steak and fillet form.

A small but steady market for dogfish (listed as grayfish) exists in New York's Fulton Fish Market where it has an ex-vessel value of 3–4 cents per pound but has gone as high as 8–10 cents per pound.[4] The fish are mostly incidental to otter trawl catches of other food fishes. The dogfish are gutted, skinned, and cut into small pieces, and sold at retail mostly to buyers of southern European extraction (Italians, Portuguese, Greeks), Chinese, and Negroes. Some retailers fry the pieces to order for "fish and chips." (Farther south on the Atlantic coast, in the Chesapeake States, the species sold as grayfish is the smooth dogfish.)

[4] Ledner, J. F., 1964. Fishery products report, N–252, Dec. 29, 1964. U.S. Bureau of Commercial Fisheries, Market News Service, New York, N.Y., 4 pp. [Unpublished processed report.]

MANAGEMENT OF THE SPECIES

The problem of the spiny dogfish as a pest of the commercial fishermen has led to a search for some method to control the species and at least reduce their numbers to the point where they would no longer constitute a problem. Many ideas have been advanced—some quite fanciful—including the usual solution to such pest problems, the payment of bounties for their capture. Unfortunately, most of the schemes suffer from a lack of, or incomplete, knowledge of the life history and habits of the dogfish.

Some of the earlier control methods proposed were based on methods used to control terrestrial pests. Atkins (1904) recounts a few suggestions offered by the public as to how the dogfish problem might be handled. Among these are the following: (1) Attach streamers, bells, chains, etc. to hundreds of dogfish and release them to frighten off the school (like belling a rat in a pack); (2) inoculate some of the dogfish with a fatal disease organism, such as had been done with rabbits in Austrialia; (3) dynamite the dogfish schools when they appear; (4) employ Government boats and men to capture the dogfish, until the plague is reduced; (5) pay a bounty to fishermen for capturing the dogfish; and (6) use long seines of strong cord, 41,000 yards or more in length, and surround the schools as is done with the schools of sharks in India.

The best control method, however, would be greater utilization of the dogfish, particularly as human food. Or, as Atkins stated it: let the public ". . . apply their teeth and eat the dogfish up."

Increased use of the species, particularly industrial utilization, carried out over a period of years, would undoubtedly reduce the numbers and keep them at a relatively low level. There is evidence that short-term programs designed to reduce the dogfish population, particularly if carried out in local areas, are not successful. Templeman (1944) notes, "In Placentia Bay alone during the 1938 attempt to reduce dogfish numbers, about 10,391,000 pounds of dogfish were caught or approx-

imately 2 or 3 million fish without any apparent diminution of the supply."

The results of increased exploitation of the North European oceanic stock of dogfish are discussed by Aasen (1961, 1963, 1964a, 1964b). In the period 1957–62, the Norwegian catch of dogfish increased by 50 percent. Returns from dogfish tagged in 1958–60 indicated an annual fishing mortality rate of 7 percent and an annual natural mortality rate of 20 percent.

During the 1961–62 fishing season, there was an annual mortality rate of 38 percent. (Aasen did not separate fishing and natural mortality.) And he reported (1964a) an average total instantaneous mortality rate of 72 percent in the years 1960–63. He interpreted the high figure as a "danger signal." A measure of catch per unit of effort for the period 1957–63 ". . . shows a heavily declining stock [of spiny dogfish]."

The evidence presented by Aasen in his several papers, and by Barraclough (1953), shows that long-term exploitation of the dogfish can produce a real reduction in their numbers. Thus, increased fishing effort on the dogfish off the United States could bring about some marked changes in the size of the population. It is not unreasonable to suspect that future fishery biologists might be called on for studies to save declining dogfish stocks in North American coastal waters.

If increased use of the dogfish is not feasible, either for food or industrial purposes, some other method of control should be investigated. A rather unique method—the sterile-male technique—has been used successfully to control the screwworm, an insect pest of cattle, and may prove of some value in the case of the spiny dogfish. The method is described by Knipling (1959) and, briefly, involves sterilizing laboratory-reared male screwworms through the use of gamma irradiation. The treated males are released in the area of infestation in the ratio of 5 to 10 times the number of normal males. Females that mate with the sterile males lay infertile eggs, thus reproduction is greatly reduced. The treatment has been successful in eliminating the pest on the island of Curacao and controlling it in Florida. Knipling states that this control method is based on the following biological principle: "The introduction of sexually sterile but otherwise sexually vigorous males, and to a lesser extent females, into the natural population of an animal species will have greater influence in reducing the biotic potential of the population than elimination of the same number of individuals from the same population by destruction or removal." The sterilization could be done either by irradiation or with chemicals.

It would be difficult at the present time to try to evaluate on a theoretical basis the sterile-male technique applied to the spiny dogfish problem. We lack some very necessary knowledge of the life history of the species. For example: (1) How many dogfish need to be sterilized to effect control (that is, how many dogfish are present in the total population), (2) how many times in its lifespan will a dogfish mate (screwworms mate once), and (3) does one male dogfish mate with more than one female in a given season?

The low fecundity of the spiny dogfish and the long period of gestation are factors very much in the favor of any control method that might be applied. But mere control is not a very satisfying solution to the problem of dogfish abundance. From a conservation standpoint it would be more desirable, of course, to find a use for what is very obviously a rich potential resource. It is possible that in future years, when additional sources of animal protein are needed for human food, we may see development of an active fishery for the species. Such a development would then remove the dogfish from the pest classification.

SUMMARY

The spiny dogfish, *Squalus acanthias*, is a small shark of the family Squalidae. It is extremely abundant locally and seasonally and has proved to be a costly nuisance to commercial fishermen in the United States.

It grows to a maximum length of 100–124 cm. and a maximum weight of 7.3–9.8 kg. The females usually are slightly larger than the males. Two sharp spines, one anterior to each dorsal fin, are the features that give the species its common name and serve to separate it readily from the smooth dogfish, *Mustelus canis*.

Although the spiny dogfish is distributed in many parts of the world, this report deals mostly with the groups found in the Northwest Atlantic. Pertinent information, however, is reported from studies of the species made in other areas.

The spiny dogfish usually is found in large schools composed of: (1) large, mature females; (2) medium-size-fish, either mature males or immature females; or (3) small, immature fish of both sexes in about equal numbers. The schools may spend considerable time in an area and then move rapidly from one area to another.

In the Northwest Atlantic they move from the southern part of their range, off North Carolina to New York, northward with the advance of the spring season. It is suspected they spend the winter offshore in deep water. In addition to the seasonal migrations, spiny dogfish take part in a daily migration, rising to or near the surface during the night and returning to the bottom during the day.

Tagging studies have had low rates of return compared with tagging studies of commercially valuable fishes. But the returns have shown that the spiny dogfish is capable of long-distance migrations—one individual travelled 4,700 miles—and is long-lived since several tagged fish were at liberty 7 to 10 years. In the New England area, the recaptures suggest that spiny dogfish school together for long periods of time and return to the same general area at about the same time of year.

Food habits studies show that spiny dogfish are primarily fish eaters but also feed on invertebrates, both swimming and bottom-dwelling forms. Clupeoids, smelts, and chimeroids were the fishes found most frequently in dogfish stomachs. They also feed on shrimp, crabs, and squids and are one of the few fishes that eat ctenophores. In general, they are considered opportunistic feeders, preying on whatever is abundant and readily available to them.

Age and growth studies based on interpretation of annulations on the dorsal spines suggest the spiny dogfish is long-lived with some individuals attaining ages of 20 to 30 years. Based on the spine readings, the growth rate is about 3½ cm. per year. Growth of tagged dogfish, however, is less, usually about 1½ cm. per year. At a given length, female dogfish are slightly heavier than male dogfish; mature and pregnant females are the heaviest and longest individuals.

It is difficult to make any analyses of the dynamics of dogfish populations because so much of the basic life history information is lacking. More is known about the natality of the species than about the mortality.

The spiny dogfish is ovoviviparous. Sex ratio of the developing fetuses is very nearly 1:1, and presumably the young are born in the same ratio. Sex ratio of the older fish varies with the sexual maturity of the individuals; in general they tend to group themselves by sex. Sexual maturity is attained by males at 80–100 cm. in length and by females at 100–124 cm.

Mating takes place during the cold months, probably on the wintering grounds, and the young are born after a 2-year development. The number of young born per female varies with location. In the Pacific it averages about 11 in the western part and about 7 in the eastern part. In the Atlantic it averages about 4 in the western part and about 3 in the eastern part. At the time of birth the young dogfish are about 20–30 cm. long.

The natural mortality of the adults apparently is low. In the Western Atlantic their principal predators are the large sharks and large bony fishes. Records of cannibalism are rare, and there are few records of marine mammals feeding on spiny dogfish. Fishing mortality, however, takes a relatively high toll.

In the United States the spiny dogfish has been exploited mostly as an industrial fish for reduction to meal and oil. Immediately preceding and during World War II, the groups on the west coast were heavily exploited for their livers, an important source of natural vitamin A. At the peak of the fishery, in 1944, more than 40 million pounds of dogfish were taken from Puget Sound. The fishery collapsed when vitamin A was synthesized in 1947, and today about 2 million pounds are landed yearly. Most dogfish are caught with otter trawls or gill nets.

There is a small and relatively steady market in the United States for dogfish as human food. Technological problems, however, have prevented it from becoming more than just locally popular. Fresh dogfish fillets have a flavor and texture somewhat resembling those of haddock. It is a popular food fish in parts of Europe.

Management of the species is indicated to reduce the damage it causes to more valuable commercial fisheries. Finding an economically attractive use for the dogfish would be the most worthwhile management method. Lacking this,

perhaps some form of biological control must be instituted. However, more detailed information is needed about the life history and biology of the spiny dogfish before any management plan can be drawn up.

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PYGMY WHITEFISH *PROSOPIUM COULTERI* IN THE NAKNEK RIVER SYSTEM OF SOUTHWEST ALASKA

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ABSTRACT

The pygmy whitefish is widely distributed throughout the lakes of the Naknek River system in southwest Alaska. It is a small abundant species in some lakes of the system and may occupy a more prominent place in the population dynamics of fishes in the Naknek system than in other geographic areas where it has been studied. Specimens were collected with a variety of sampling gear including gill nets, tow nets, otter trawls, and seines. Pygmy whitefish occurred in all benthic habitats from shallow littoral depths to bathybenthic areas. Seasonally in certain age groups and in certain areas they occurred in limnetic areas of lakes and in streams. In the Naknek system, 18 species, including the young of commercially valuable sockeye salmon and the closely related round whitefish, were ecological associates of pygmy whitefish.

Two populations, one in South Bay of Naknek Lake and the other in Brooks Lake, were studied in detail. The oldest and largest pygmy whitefish collected was an age V 163-mm. female from South Bay. An age III 83-mm. female was the oldest and longest specimen from Brooks Lake. Length frequency distributions from other lakes were intermediate between these extremes. Growth rates were back calculated from polynomial body length–scale length equations for Brooks Lake and South Bay populations.

Dipteran insects were the principal foods eaten by pygmy whitefish in South Bay. Crustacean plankton dominated their diet in Brooks Lake. In other areas insects and zooplankton were about equal in importance. Growth and insect consumption were correlated positively.

Spawning occurs in November and December, apparently only at night. South Bay fish spawn in lower Brooks River. Eggs in ripe females from South Bay averaged 2.4 mm. in diameter, and the ovaries were 16.5 percent of the body weight. The fork length-fecundity relation of Naknek system pygmy whitefish has the equation

$$\text{Log } E = -2.9552 + 2.7513 \text{ Log } L$$

Both sexes mature earlier in Brooks Lake than in South Bay.

Slow growth, low fecundity, and short life characterize pygmy whitefish in Brooks Lake. These factors are compensated for in part by early maturity and probably by a low mortality from fertilized egg to maturity. The wide range of pygmy whitefish populations in the Naknek system probably reflects adaptive responses of a highly plastic species to the wide variety of environmental characteristics found in different lakes of the system.

Pygmy whitefish, *Prosopium coulteri* (Eigenmann and Eigenmann), are widely distributed throughout lakes of the Naknek River system in southwest Alaska (fig. 1). These lakes, which are important fresh-water rearing areas for juvenile sockeye salmon, *Oncorhynchus nerka* (Walbaum), are studied by the Bureau of Commercial Fisheries to determine factors limiting fresh-water production of this highly important commercial species. These studies embrace a variety of limnological and biological research, including interspecific relations of fishes associated with juvenile salmon.

Pygmy whitefish are apparently the most abundant species in some lakes of the Naknek system, and it is possible that they may compete directly

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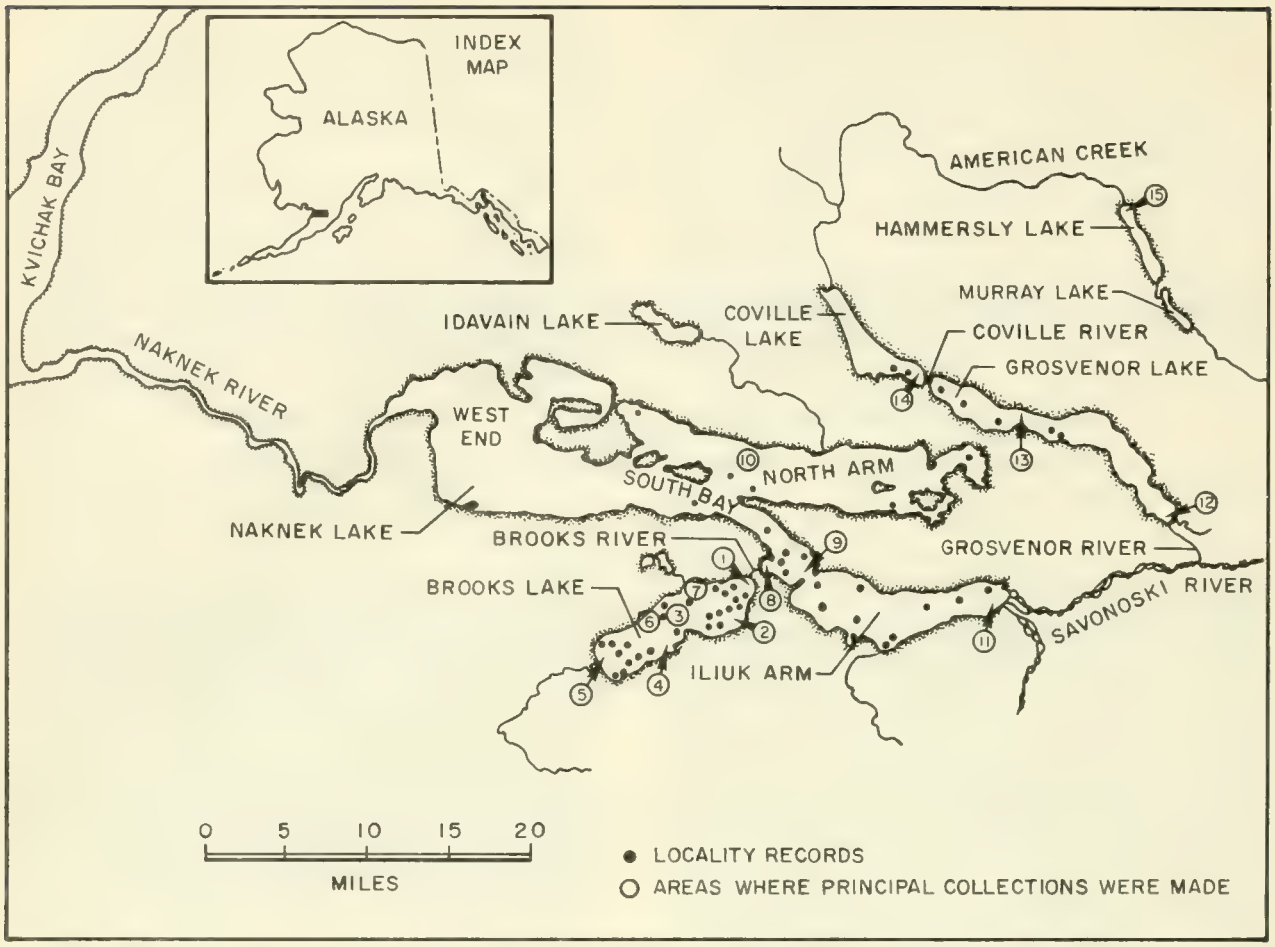

FIGURE 1.—Naknek River system of southwest Alaska, showing areas where pygmy whitefish were collected. Dots represent locality records; circled numbers are locations where 10 or more pygmy whitefish were collected in a specific sampling effort.

or indirectly with juvenile sockeye salmon for food or space. Other fishes, for instance the threespine stickleback (*Gasterosteus aculeatus*), have also been characterized as actual or potential competitors with juvenile sockeye salmon (Krogius and Krokhin, 1948; Greenbank and Nelson, 1959; and Burgner, 1960). Pygmy whitefish may also act as a buffer between salmon predators and young salmon.

There is relatively little literature concerning pygmy whitefish, and specific studies on the biology of this species are few. They were discovered in British Columbia in 1892 and were first collected in Alaskan waters in 1912 (Kendall, 1917). Although locality and life history data accumulated for several years (Snyder, 1917; Kendall, 1921; Schultz, 1941; and Wynne-Edwards, 1947 and 1952), published material was based on few specimens. Meyers (1932) reported on 21 specimens from Chignik River on the Alaska Peninsula, and Weisel and Dillon (1954) reported on 23 pygmy whitefish from western Montana. Eschmeyer and Bailey (1955) collected 1,623 pygmy whitefish from Lake Superior during a 2-year study and reported the discovery of a relatively large population in the lake and described its morphology and life history. Comparisons were made with previous collections from the Pacific slope. McCart (1963) has recently studied the growth and morphology of pygmy whitefish from several British Columbia lakes.

Pygmy whitefish were first collected in the Naknek River system at Brooks Lake in 1957, and observations in Brooks Lake have continued since

then.[1] Beginning in 1961 and continuing through 1963, observations were extended throughout the Naknek system. More than 10,000 specimens have been collected by various methods since 1961.

The present study was undertaken to investigate the distribution, age and growth, food habits, reproduction, and general life history of pygmy whitefish in the Naknek system. Emphasis was placed on determining the relation of pygmy whitefish biology to that of other fishes in the system, particularly the sockeye salmon.

STUDY AREA

The Naknek River system, much of which lies within Katmai National Monument, consists of seven interconnecting lakes: Hammersly, Murray, Coville, Grosvenor, Brooks, Idavain, and Naknek. These lakes drain into the northeast side of Bristol Bay through the Naknek River (fig. 1). All are glacial in origin, dating from Wisconsin times (Muller, 1952; and Karlstrom, 1957). Naknek Lake comprises three major basins and a shallow outwash plain. The basins, Iliuk Arm, North Arm, and South Bay, and the outwash plain, West End, will be referred to hereafter without reference to Naknek Lake. The maximum depths are not known for Murray, Idavain, or Hammersly Lakes. The other lakes vary between a maximum depth of 53 m. in Coville Lake and 173 m. in Iliuk Arm.

The lakes and basins of the Naknek system include a broad range of environmental types. Most of them are oligotrophic and usually have ice cover from December through early May. Iliuk Arm frequently does not freeze over completely, probably because of its depth and excessive turbidity, which is due to glacial melt water and volcanic ash. In Iliuk Arm, Secchi disk visibility is generally less than 0.5 m., while in the other basins and lakes it ranges between 3 and 12 m. A horizontal turbidity gradient occurs in South Bay, increasing in intensity toward Iliuk Arm. Thermal gradients commonly exist, although classical thermoclines develop only occasionally and are unstable. The waters are slightly alkaline, and oxygen levels remain at or near saturation at all depths measured throughout the year. The basic limnology of lakes in the Naknek River system is described in detail elsewhere.[2]

MATERIALS AND METHODS

Most pygmy whitefish were collected in the Naknek system with small otter trawls, tow nets, beach seines, and small-meshed gill nets. A few specimens were collected with fyke nets and floating lake traps and by divers using hand nets. These same methods were used to sample juvenile sockeye salmon in various stages of their freshwater life. Heard (1962) described the small-meshed gill nets, and the three other principal types of gear are described below. All mesh sizes are given in stretch measure.

The otter trawls were Gulf Coast shrimp try-trawls about 6 m. long, 2.6 m. wide, and 0.6 m. deep. The cotton webbing varied from 50.8-mm. mesh in the front section to 25.4-mm. in the cod section, with a 13-mm. mesh cod liner. The footrope was weighted with a 19-mm. mesh chain, and the otter doors were 30.5 by 45.7 cm. Except for use of a tow cable guide ring on the transom, our use of these trawls behind an outboard skiff was basically the same as described by Baldwin (1961).

Trawl drags varied in time, in length of drag, and in depth. Generally they were between 8 and 15 minutes long and covered from 325 to 1,000 m. The trawls were fished effectively for pygmy whitefish to depths of 79 m.

The tow nets were 3.1 m. in diameter and 6.9 m. long, and they were used generally at night in limnetic (offshore or open water) portions of the lakes. They were towed behind two outboard skiffs with the top of the net at the surface or 3.1 m. deep. A standard tow was 492 m. Mesh sizes of nylon webbing varied from 38 mm. at the net opening to 3 mm. in the cod end. Burgner (1960) describes the construction and general use of this net. A 1-m. tow net such as that described by Johnson (1956) was used to collect one sample of pygmy whitefish in Brooks Lake.

Three types of beach seines were used. The two principal types, which were set in a semicircular pattern from shore with an outboard skiff, were 3.1 m. deep and 32.8 or 42.6 m. long. The 32.8-m. seine consisted solely of 3 mm. webbing, and the

[1] The annual field reports of the research operations at Brooks Lake (1957–62) are on file at the Bureau of Commercial Fisheries Biological Laboratory, Auke Bay, Alaska.

[2] Hartman, Wilbur L., and Robert L. Burgner. The limnology of sockeye salmon nursery lakes in southwest Alaska. The manuscript is filed in the U.S. Bureau of Commercial Fisheries Biological Laboratory, Auke Bay, Alaska.

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42.6-m. seine consisted of a center section (9.8 m. long) of 6-mm. webbing and two end sections (16.4 m. long) of 12-mm. webbing. The third type was 1 m. deep with 3-mm. webbing and was either 3.1 or 6.1 long.

Most collections of pygmy whitefish were preserved and processed for various biological data; specimens from the other collections were discarded after the catch was recorded. Fork lengths were measured in millimeters and weights in tenths of grams. Most collections were preserved in 10-percent formalin for at least 48 hours before processing. The conversion factor of 0.977 to account for shrinkage was applied to length data on one group of fresh specimens. All lengths given are preserved lengths or equivalents. Because Eschmeyer and Bailey (1955) presented their pygmy whitefish data in total lengths, we determined factors for converting fork lengths to total lengths. Fork length times 1.0777 equals total length for specimens shorter than 100 mm., and fork length times 1.0845 equals total length for specimens longer than 100 mm.

Biological information determined from individual specimens included age and growth determinations, stomach content analyses, and reproductive data. Age and growth were analyzed from scale samples and length frequencies. Stomach content analyses were made either on all of the specimens or on random samples from different collections. The occurrence of food items was determined for individual fish, while volumetric analyses were made by combining food items from all fish in a specific collection. Sex ratios and age and length at maturity were determined for random samples or for all fish in different collections. Egg content was determined for 85 females by total count.

DISTRIBUTION AND ABUNDANCE OF PYGMY WHITEFISH

Pygmy whitefish have the greatest discontinuous range of any fresh-water fish in North America according to Eschmeyer and Bailey (1955). In addition to its occurrence in Lake Superior of the Atlantic slope, this species has been recorded from the Columbia River drainage in Washington, Montana, and British Columbia (Schultz, 1936; Weisel and Dillon, 1954) and from the Fraser, Skeena, Yukon, and Mackenzie River systems of the Pacific and Arctic slopes (Carl, Clemens, and Lindsey, 1959). It also occurs in both Pacific and Bering Sea drainages of southwest Alaska, having been reported from the Nushagak (Snyder, 1917), Chignik (Kendall, 1917), Naknek (Merrell, 1964), and Kvichak (personal communication, Ole A. Mathisen and O. E. Kerns) River systems. Pygmy whitefish probably occur in other Bristol Bay river systems on the Alaska Peninsula, such as the Ugashik and Egegik, where large lakes appear to provide suitable habitat.

Eschmeyer and Bailey (1955) concluded that the present disjunct populations of pygmy whitefish are all referable to the same species and most likely represent relicts of a continuously distributed species in late Pleistocene that survived in deep lakes after the retreat of Wisconsin glaciation. McCart (1963) compared meristic and morphological variation in pygmy whitefish from British Columbia with those from other areas and found the species to be highly variable both within and between populations.

The sizes attained by pygmy whitefish in different geographic areas varied, most likely because of differences in growth rates related to different environments. The maximum size reported from Lake Superior was 149 mm. Carl, Clemens, and Lindsey (1959) reported a population of "giant" pygmy whitefish in Maclure Lake, British Columbia. McCart (1963) found pygmy whitefish in this lake as large as 262 mm. The maximum sizes in the Naknek system varied considerably between lakes, ranging from 84 mm. in Brooks Lake to 163 mm. in South Bay (fig. 2).

NAKNEK SYSTEM

Pygmy whitefish are widely distributed throughout the Naknek system and were collected in every major water area in the system except Idavain and Murray Lakes and West End (table 1). No attempt was made to collect them in Idavain Lake, and only one small-meshed gill-net set, which was unproductive, was made in Murray Lake. Pygmy whitefish may have been collected in 1962 from the West End in tow nets, but the discarded specimens were recorded on field data sheets only as "whitefish." It is likely that they do occur in these three major areas, however.

The abundance of pygmy whitefish varied throughout the system. The distribution is best

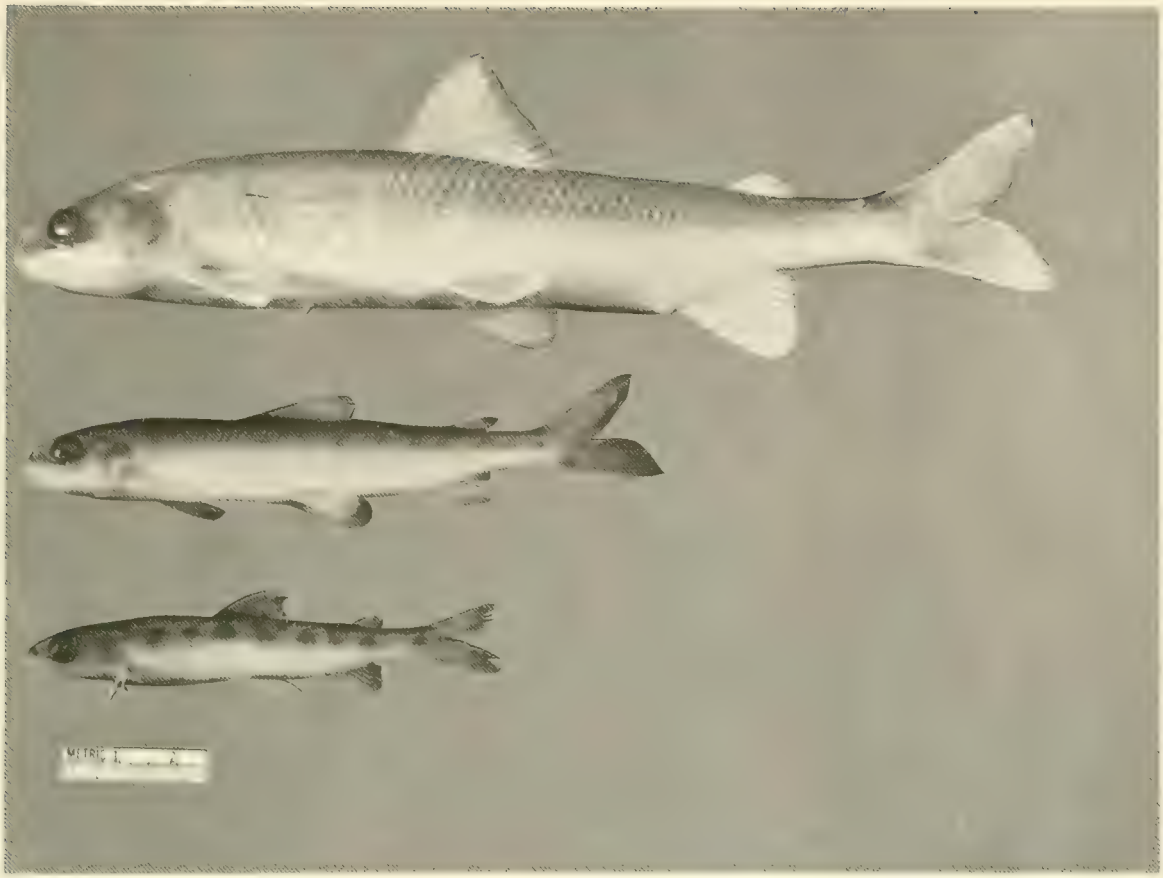

FIGURE 2.—Pygmy whitefish from the Naknek system. From top to bottom: 5-year-old mature female, 163 mm. long, collected November 9, 1962, in South Bay; 2-year-old immature female, 98 mm. long, collected November 9, 1962, in South Bay; 3-year-old mature female, 76 mm. long, collected November 7, 1962, from Brooks Lake.

known in Brooks Lake where the greatest sampling effort was expended. Pygmy whitefish were collected in all sections of Brooks Lake, and two areas of heavy abundance were found at opposite ends of the lake (areas 1 and 5 (fig. 1)). They also occurred throughout South Bay and Iliuk Arm. A concentration of this fish apparently occurs in the semiprotected bay of South Bay near the mouth of Brooks River and in the upper end of Iliuk Arm. The known distribution of pygmy whitefish in North Arm is spotty, but it is believed to be widely distributed in this basin. In 1962 and 1963, small whitefish were not specifically identified on field collection sheets of seine records from that basin. We suspect that at least some of these were pygmy whitefish. In Grosvenor Lake, pygmy whitefish were collected in most areas of the lake; but, in Coville Lake, they were collected only from the east end of the lake. The one Hammersly Lake collection was made near the lake outlet.

The most widely used sampling gear throughout the system was tow nets, which was used in open-water limnetic areas, primarily to sample juvenile sockeye salmon. Otter trawls, gill nets, and seines, which were more effective than tow nets in sampling pygmy whitefish, were used to different degrees in different areas (table 1). The unknown vulnerability of pygmy whitefish to different types of gear and the unequal use of each type in various lakes and basins should be kept in mind when considering relative abundance.

On the basis of the number of specimens obtained in other geographic areas by previous collectors, populations of pygmy whitefish may occupy a more dominant role in the overall fish population structure in parts of the Naknek system than in other areas. In the Lake Superior study, the greatest single collection of pygmy

TABLE 1.—*Sampling efforts* [1] *with otter trawls, tow nets, small-meshed gill nets, and beach seines in Naknek system and percent of samples yielding pygmy whitefish, 1961–63*

Sampling area and year	Otter trawl		Tow net		Gill net [2]		Seine	
	Sampling efforts	Samples with pygmy whitefish	Sampling efforts	Samples with pygmy whitefish	Sampling efforts	Samples with pygmy whitefish	Sampling efforts	Samples with pygmy whitefish
	Number	*Percent*	*Number*	*Percent*	*Number*	*Percent*	*Number*	*Percent*
Brooks Lake:								
1961	79	33	108	31			3	33
1962	60	43	154	8	2	100	28	36
1963	4	75	40	8	9	78	4	75
Coville Lake:								
1961			60	0			5	[3] 0
1962	15	0	41	2	1	100	37	[3] 24
1963	5	0	47	2	3	0		
Grosvenor Lake:								
1961			101	3			7	[3] 0
1962	21	10	53	4			26	[3] 12
1963	1	100	20	5				
Naknek Lake:								
South Bay:								
1961	1	100	57	4			6	33
1962	8	75	61	10	3	100	47	68
1963	2	100	39	3	6	100	6	83
Iliuk Arm:								
1961	2	0	49	2	2	100	4	50
1962			72	6			12	58
1963			36	6	2	50	2	100
North Arm:								
1961			32	0	3	100	8	0
1962			94	1	3	100	24	[3] 0
1963			12	0	1	100	5	0
West End:								
1961	5	0	21	0				
1962			52	[3] 0			5	0
1963			44	0				
Hammersly Lake:								
1962					1	100		
Murray Lake:								
1962					1	0		
Brooks River:								
1963	4	100					2	100

[1] A sampling effort equals one trawl haul, tow net haul, gill net lift, or individual seine haul.
[2] Includes only those gill net sets with mesh sizes 1-inch stretch measure or smaller.
[3] Not including sampling efforts containing unidentified small whitefishes which may have included pygmy whitefish.

whitefish was 171 specimens taken in an otter trawl in Siskiwit Bay (Eschmeyer and Bailey, 1955). Our largest single collection was 1,701 specimens taken in a beach seine haul on August 14, 1962, in Brooks Lake (table 2). The largest Lake Superior collection had about 80 percent age 0+ fish, while the largest Brooks Lake collection had 100 percent age 0+ fish. Our second largest collection was made July 10, 1962, by a trawl drag in Brooks Lake that yielded 1,567 age I+ and age II+ fish. A beach-seine haul in South Bay on August 4, 1962, yielded 964 specimens (table 2). Of these, 962 were age I+ and older. All of the 1961–63 collections of pygmy whitefish from the Naknek system in which 10 or more specimens were caught in a sampling effort are listed by date, area, gear, depth, and number of specimens in table 2.

ECOLOGICAL AND SEASONAL DISTRIBUTION

Pygmy whitefish occupy a wide variety of ecological habitats in the Naknek system. They were caught not only in benthic habitats, ranging from a depth of 168 m. (in Iliuk Arm and North Arm) to littoral areas less than 1 m. deep, but also in limnetic areas at or near the surface over deep water and in several streams.

The capture of pygmy whitefish in littoral areas with seines and trawls and in limnetic areas with tow nets was somewhat unexpected. In Lake Superior, Eschmeyer and Bailey (1955) caught pygmy whitefish only in benthic areas below 10 fathoms. Except for six specimens caught in gill nets, all Lake Superior pygmy whitefish were caught in otter trawls.

Most littoral catches of pygmy whitefish in the Naknek system were made at the northeast end of Brooks Lake and in a semiprotected bay in South Bay (areas 1 and 8, fig. 1). Part of this littoral area in Brooks Lake consisted of a shallow sandy shelf 1 to 2 m. deep that extended 300 to 500 m. into the lake. This shelf is subject to heavy wave action and is barren of vegetation except for small patches of *Ranunculus* sp. Large schools of age 0+ pygmy whitefish were observed by biologists

TABLE 2.—*Collections of pygmy whitefish from the Naknek system in which 10 or more specimens were caught per sampling effort [1] by area, gear, depth, and number of specimens, 1961–63*

Sampling area and date	Numbered area [2]	Type of gear	Depth	Total specimens caught
			Meters	*Number*
Brooks Lake:				
July 17, 1961	1	Otter trawl	8	290
July 18, 1961	7	do	12	11
July 20, 1961	1	do	2	89
July 21, 1961	2	do	3	32
Aug. 7, 1961	4	do	5	150
Aug. 8, 1961	5	do	5	308
Aug. 8, 1961	5	do	8	344
Aug. 10, 1961	5	do	15	12
Aug. 10, 1961	5	do	32	10
Aug. 11, 1961	1	Tow net (3.1 m.)	0–3.1	16
Aug. 11, 1961	2	do	0–3.1	321
Sept. 1, 1961	1	do	0–3.1	10
Sept. 14, 1961	1	Otter trawl	5	96
Sept. 26, 1961	6	Tow net (3.1 m.)	3.1–6.1	10
June 29, 1962	1	Otter trawl	4	70
June 29, 1962	1	do	10	425
July 10, 1962	1	do	8	1,567
July 11, 1962	5	do	2	88
July 22, 1962	1	do	8	18
July 22, 1962	1	do	8	46
July 23, 1962	1	Tow net (1-m.)	0–1	168
July 26, 1962	7	Otter trawl	5	40
July 27, 1962	2	do	3	69
Aug. 10, 1962	4	Seine	2	24
Aug. 10, 1962	5	do	2	88
Aug. 10, 1962	5	do	2	15
Aug. 10, 1962	5	do	2	36
Aug. 14, 1962	1	do	1	1,701
Sept. 14, 1962	1	Otter trawl	8	15
Nov. 7, 1962	1	do	8	306
Nov. 8, 1962	1	Gill net	12	67
Nov. 8, 1962	2	do	3	11
July 2, 1963	1	Hand net	1	17
July 8, 1963	1	Seine	1	65
July 16, 1963	1	do	1	17
July 22, 1963	3	Gill net	66	14
July 22, 1963	3	Otter trawl	65	10
July 26, 1963	3	Gill net	78	10
Aug. 7, 1963	1	Seine	1	18
Aug. 9, 1963	3	Gill net	78	18
Aug. 20, 1963	3	do	[3] 75	11
Dec. 16, 1963	1	do	12	29
South Bay:				
July 15, 1962	8	Seine	2	46
July 22, 1962	9	do	3	36
South Bay—Con.				
July 23, 1962	9	Seine	3	16
July 23, 1962	9	do	3	25
July 23, 1962	9	do	3	16
July 23, 1962	9	do	3	53
July 23, 1962	9	do	3	10
Aug. 4, 1962	8	do	2	542
Aug. 4, 1962	8	do	2	16
Aug. 4, 1962	8	do	2	22
Aug. 4, 1962	8	do	2	345
Aug. 4, 1962	8	do	2	11
Aug. 4, 1962	8	do	2	964
Aug. 24, 1962	8	do	2	96
Sept. 26, 1962	8	do	2	148
Nov. 9, 1962	8	do	2	124
Nov. 10, 1962	8	Gill net	8	116
Apr. 16, 1963	8	do	7	20
May 30, 1963	8	do	8	12
June 14, 1963	8	Seine	1	12
July 11, 1963	8	do	1	144
Oct. 29, 1963	8	Gill net	8	33
Nov. 5, 1963	8	do	8	56
Dec. 12, 1963	8	do	3	81
Brooks River:				
July 27, 1963	8	Seine	1	458
Aug. 24, 1963	8	Otter trawl	1	178
Aug. 24, 1963	8	do	1	18
Aug. 25, 1963	8	do	1	200
Aug. 25, 1963	8	do	1	150
Iliuk Arm:				
July 9, 1963	11	Seine	3	12
July 27, 1963	11	do	3	27
North Arm:				
July 22, 1962	10	Gill net	169	10
Aug. 9, 1962	10	do	169	21
Coville Lake:				
June 7, 1962	14	Seine	2	12
June 7, 1962	14	do	2	10
June 9, 1962	14	do	2	10
July 12, 1962	14	do	2	12
Grosvenor Lake:				
June 30, 1962	12	do	2	48
Aug. 5, 1962	13	Otter trawl	8	54
Aug. 19, 1963	12	do	7	96
Hammersly Lake:				
Aug. 20, 1962	15	Gill net	20	12

[1] A sampling effort is an individual trawl haul, tow net haul, beach seine haul, or gill net lift.
[2] See figure 1.
[3] Gill net was buoyed so that it was fishing horizontally 3 m. off the bottom in water 78 m. deep.

skin diving along this shelf during June, July, and August, 1962 and 1963. These fish were routinely caught with seines or hand nets. On July 23, 1962, 168 age 0+ pygmy whitefish were caught on the edge of this shelf in a 1-m. tow net (table 2). This particular catch was made in an area where Arctic Terns (*Sterna paradisaea*) were feeding on small fishes near the surface, presumably pygmy whitefish. Littoral collections in South Bay were made during April, May, June, July, August, September, October, November, and December in either 1962 or 1963 (table 2). Pygmy whitefish apparently remain in the littoral area of this bay throughout most of the year. No sampling was attempted during late winter or early spring.

In addition to the above areas, substantial numbers of pygmy whitefish were also caught in littoral areas in the narrows between South Bay and Iliuk Arm, at the upper end of Iliuk Arm, and near the outlets of Grosvenor and Coville Lakes (areas 9, 11, 12, and 14, fig. 1).

Pygmy whitefish in the Naknek system apparently are associated with the benthic zone at all lake depths. Benthic collections have been made from all depths in Brooks Lake with seines, trawls, or gill nets and from shallow shoreline and the deepest areas of North Arm and Iliuk Arm with seines and gill nets. This distribution differs from the bathybenthic distribution found in Lake Superior (Eschmeyer and Bailey, 1955) and the intermediate benthic distribution found in four British Columbia lakes (McCart, 1963). In each of these studies, pygmy whitefish were sampled primarily with one collecting gear—trawls in Lake Superior and gill nets in British Columbia.

Although pygmy whitefish are generally associated with the benthic zone, concentrations of them were typically spotty. A series of 11 conse-

cutive seine hauls made along a 600-m. stretch of beach in South Bay on August 4, 1962 (table 3), shows that catches are variable and suggests that pygmy whitefish are frequently grouped in large schools. Approximately 80 percent of the pygmy whitefish collected throughout the Naknek system came from specific sampling efforts that yielded 100 or more specimens.

TABLE 3.—*Age 0+ and older pygmy whitefish caught in 11 consecutive seine hauls in South Bay, August 4, 1962*

Seine haul number	Fish per haul	
	Age 0+	Age 1+ and older
	Number	*Number*
1	0	542
2	1	0
3	1	3
4	2	3
5	12	4
6	20	2
7	0	0
8	0	0
9	4	341
10	7	3
11	2	962

Underwater observations on the schooling and feeding behavior in lower Brooks River indicated that pygmy whitefish are frequently grouped in schools of several thousand fish. Fishes in these schools were evenly spread out over several meters of stream bottom. Individuals fed independently of other fish, and the undisturbed school of fish would slowly move from one area to another. When disturbed by an observer or predator, schools of pygmy whitefish in Brooks River became tightly grouped.

The distribution of age 0+ pygmy whitefish, particularly in Brooks Lake, changes in late summer. Many of these young whitefish remain in littoral areas on the sandy shelf along the northeast shoreline of Brooks Lake throughout much of the summer, but by mid-August they begin disappearing. They are scarce in this area in September. During the same period, limnetic catches of pygmy whitefish in tow nets increase. Age 0+ sockeye salmon in Wood River Lakes behave similarly (Burgner, 1960). Naknek system age 0+ sockeye salmon also show this behavior, although it is not as pronounced. The reasons for this fall change in distribution of young pygmy whitefish are not known. The autumn lake turnover, changes in diet attendant with shifts in food supplies, or other limnological changes may be involved. During the fall, weather on the Alaska Peninsula is characterized by severe storms with gale winds. The resultant heavy wave action may tend to disperse young pygmy whitefish from littoral areas.

About 95 percent of the pygmy whitefish caught with tow nets in all lakes and basins were age 0+ fish. In 1961 tow nets were used in Brooks Lake from mid-August throughout September, while otter trawls were used primarily from mid-July to mid-August. A comparison of length frequencies of pygmy whitefish caught in limnetic areas with tow nets with those caught in benthic areas with trawls during these periods indicates (fig. 3)

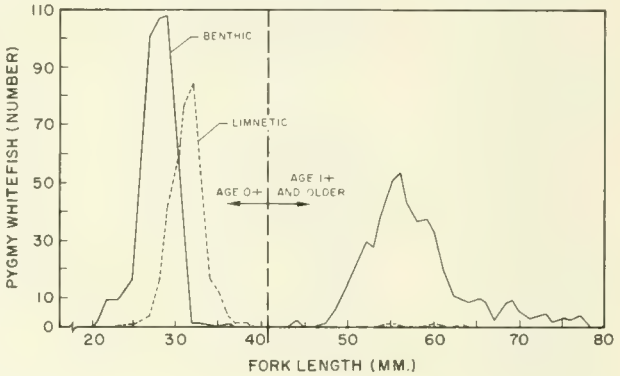

FIGURE 3.—Comparison of length frequencies of pygmy whitefish caught from mid-July to mid-August in benthic areas with otter trawls with those caught from mid-August through September in limnetic areas with 3.1-m.-diameter tow nets, Brooks Lake, 1961.

that while both age 0+ and older fish were caught in the benthic zone, most of those caught in the limnetic zone were age 0+. Differences in the selectivity of the two gears could have affected these catches; however, we do not feel trawls were selectively collecting older, larger pygmy whitefish since comparative catches of other fishes suggest that larger specimens are usually caught in tow nets. Our interpretation of these data is that fewer age 1+ and older pygmy whitefish were present in limnetic areas than in benthic areas. Differences in length frequencies of age 0+ fish shown in figure 3 are due to sampling periods and not to differences in size of fish caught in separate ecological areas or with different sampling gear. In 1962 and 1963 when tow nets were used in Brooks Lake throughout July and August, no pygmy whitefish were caught in limnetic areas

until late August. Some age 0+ fish may have been present in limnetic areas before this time, although they probably would have been too small to capture in the available gear. Few tow net hauls were made in September, except in Brooks Lake in 1961.

Although no permanent stream populations of pygmy whitefish are known to exist in the Naknek system, large numbers seasonally occupy the lower 100 to 400 m. of Brooks River. These fish are part of the South Bay population (area 8, fig. 1) and do not go above a rapids area below Brooks River falls. They occupy lower Brooks River from late June to early September for feeding and from mid-November to mid-December for spawning. Feeding pygmy whitefish in Brooks River characteristically occupy neither the fastest moving nor the slowest moving water, but seem to prefer a moderate current adjacent to a faster one.

A few pygmy whitefish have been collected or observed in other streams in the system. With the possible exception of an annual downstream drift of spent fish in midwinter, these collections apparently represent only sporadic downstream movements of fish from Brooks, Coville, and Grosvenor Lakes. Underwater surveys of upper Brooks River from May through November and of Coville River from May through August revealed that pygmy whitefish did not occupy these streams during this period.

ASSOCIATED FISHES

Nineteen species of fishes were collected with pygmy whitefish in various parts of the system. The percent frequency occurrence of these species (table 4) provides a basis for discussing associated species. Throughout the system the cottids *Cottus aleuticus* Gilbert and *C. cognatus* Richardson were the most frequent associates, occurring in 55 percent of all sampling efforts that yielded pygmy whitefish (table 4). Juvenile sockeye salmon were the second most frequent associates, occuring in 42 percent of the samples. Next in frequency of association with pygmy whitefish were ninespine sticklebacks, threespine sticklebacks, round whitefish, and least cisco (table 4). The greatest number of sympatric associates in a specific area was 17 species in South Bay.

Certain fishes in the Naknek system were not caught with pygmy whitefish in all lake areas. Least cisco, humpback whitefish, pond smelt, and longnose sucker, were collected widely in other parts of the system but not in Brooks Lake. Alaska blackfish, abundant in Brooks Lake, were not collected in South Bay or Iliuk Arm. Differences in sampling gear and effort may account for species not being caught in certain areas.

The two most common associates of pygmy whitefish in Lake Superior were cottids and ninespine sticklebacks (Eschmeyer and Bailey, 1955). Round whitefish, which were never collected in association with pygmy whitefish in Lake Superior, occurred in 17 percent of the Naknek system samples yielding pygmy whitefish. These whitefishes were collected together in six of eight major lakes, basins, or streams (table 4). This apparent difference in association between pygmy whitefish and its closest relative in Lake Superior

TABLE 4.—*Percent frequency occurrence of associated fishes in sampling efforts* [1] *that yielded pygmy whitefish*

Species	Brooks Lake	South Bay	Iliuk Arm	North Arm	Coville Lake	Grosvenor Lake	Hammersly Lake	Brooks River	All areas combined
	Percent	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*
Cottid, *Cottus* spp.	60	53	38	63	67	42	100	17	55
Sockeye salmon, *Oncorhynchus nerka* [2]	35	41	71	25	67	58		33	42
Ninespine stickleback, *Pungitius pungitius*	39	36	10	62	25				33
Threespine stickleback, *Gasterosteus aculeatus*	29	24	38	38	92	17			31
Round whitefish, *Prosopium cylindraceum*	7	29	29	50		8		67	17
Least cisco, *Coregonus sardinella*		20	52	38				33	12
Alaska blackfish, *Dallia pectoralis*	18								9
Pond smelt, *Hypomesus olidus*		15	38		8				8
Arctic lamprey, *Lampetra japonica*	10	2							6
Lake trout, *Salvelinus namaycush*	1	3	14	38	8			100	4
Arctic grayling, *Thymallus arcticus*	2	11						17	4
Humpback whitefish, *Coregonus pidschian*		3	10	50					3
Coho salmon, *Oncorhynchus kisutch* [2]	3	3		13				17	3
Arctic char, *Salvelinus alpinus*		5	5	25			100		3
Rainbow trout, *Salmo gairdneri*	2	3						100	2
Dolly Varden, *Salvelinus malma*		9							2
Longnose sucker, *Catostomus catostomus*		3	14	13					2
Northern pike, *Esox lucius*			14						1
Burbot, *Lota lota*		2							T

[1] Sampling efforts of all gears were combined for each area, then for all areas; see table 1 for total sampling effort by gear and area.
[2] Juveniles only.

and the Naknek system may be related to the use of only trawls in Lake Superior and several gears in the Naknek system. In the present study few round whitefish were captured in trawls. McCart (1963), using gill nets, found little or no association between pygmy whitefish and mountain whitefish *Prosopium williamsoni* (Girard) or lake whitefish *Coregonus clupeaformis* (Mitchill) in Cluculz and Tacheeda lakes, British Columbia.

AGE AND GROWTH

BODY-SCALE RELATION

The relation between body length and the anterior scale radius (mm. multiplied by 80) was determined for 456 pygmy whitefish from Brooks Lake and 500 from South Bay. Data from both lakes indicate this relation is highly sigmoid. Rounsefell and Everhart (1953, p. 324) suggest that problems of curvilinearity can be solved by omitting the earliest years and back calculating only those ages that do not deviate appreciably from linearity. The persistence of a curvilinear body–scale relation in the older age groups of Naknek system pygmy whitefish prevented any linear treatment of older fish. Also, these fish are relatively short lived, reaching a maximum age of 3 years in Brooks Lake and 5 years in South Bay. Age was determined from scale annuli, which, excluding scales from a few older fish, were not difficult to locate.

Fourth degree polynomial equations were found, excluding highly spurious intercepts, to fit fairly closely the empirical data for the body–scale relations of Brooks Lake and South Bay pygmy whitefish. These equations were calculated from individual pairs of body–scale observations. Mean body lengths for each scale radius are plotted against the calculated relations for both areas (figs. 4 and 5). Body length at scale formation is apparently between 22 and 27 mm. as determined by: (1) staining small fish for the first evidence of scale development and (2) calculating the intercept for collections of age 0+ fish after scale development. Separate equations were necessary for the Brooks Lake and South Bay collections because of strikingly different growth rates in the

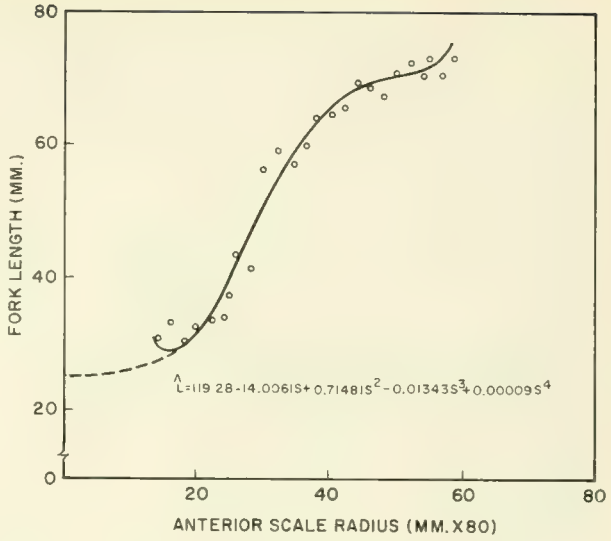

FIGURE 4.—Body length–scale radius relation of pygmy whitefish in Brooks Lake. Solid line is calculated equation; points represent mean body lengths for given scale radii; dashed line connects estimated intercept of 25 mm. with the logical portion of calculated curve.

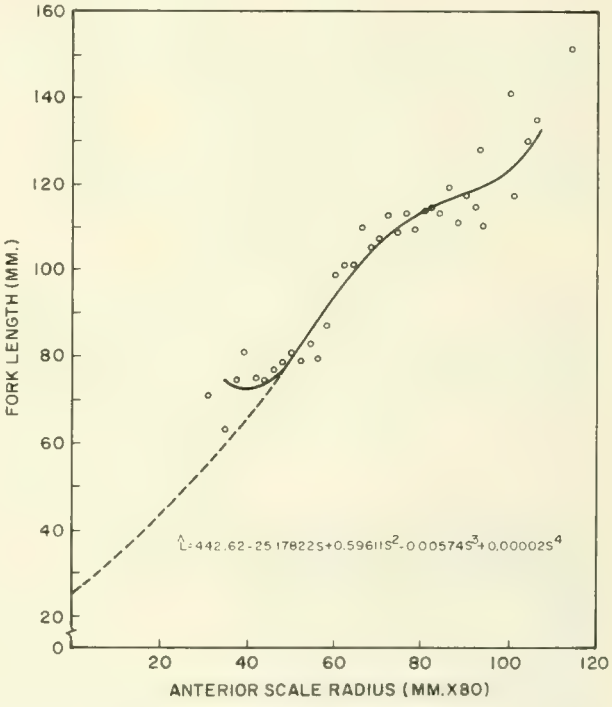

FIGURE 5.—Body length–scale radius relation of pygmy whitefish in South Bay. Solid line is calculated equation; points represent mean body lengths for given scale radii; dashed line connects estimated intercept of 25 mm. with the logical portion of calculated curve.

two populations.[3] Growth rates were back calculated from these quartic equations.

CALCULATED GROWTH

Fork lengths attained at each year of life and the annual increments were calculated by sex for 330 pygmy whitefish from Brooks Lake (table 5) and 779 from South Bay (table 6). A comparison of these growth rates reveals that pygmy whitefish grew considerably faster in South Bay than in Brooks Lake. The largest pygmy whitefish collected from Brooks Lake was an 84-mm. mature female that had just completed its third growing season. Two slightly older (III+) but smaller, slower growing females were collected from Brooks Lake. In South Bay the largest and oldest pygmy whitefish was a 163-mm. age V mature female.

During their first year of life, males in Brooks Lake grew slightly faster than females. In subsequent years in Brooks Lake and in all years in Naknek Lake, females consistently grew at a faster rate than males (tables 5 and 6). Males in Lake Superior grew slightly faster than females during the first year, grew at about the same rate as females during the second year, and grew slower than females during later years. Male pygmy whitefish in Lake McDonald, Mont., grew faster in their first year but slower than females in subsequent years, while females in Bull Lake, Mont., grew faster in all years (Eschmeyer and Bailey, 1955). With minor variations, these growth patterns are similar to those reported by McCart (1963) for pygmy whitefish in MacLure, McLeese, Cluculz, and Tacheeda Lakes, British Columbia. Males grew at about the same rate as females for the first 2 years, after which females consistently grew faster than males.

[3] Additional study is needed to understand fully the curvilinear body–scale relation of these whitefish. Few specimens have been collected from South Bay as small as the age I and II fish from Brooks Lake with usable scales. Obviously the calculated curve for South Bay fish below 75 mm. is not biologically valid. With adequate data the lower portion of the South Bay curve could approach the Brooks Lake curve for the same size fish, in which case a single equation might express the body–scale relation for both populations. The problem is aggravated by the ease with which small pygmy whitefish lose their relatively large scales. Also, South Bay fish grow as large in 1 year as Brooks Lake fish do in 2 years, and it is not known what effect different growth rates between populations or between year classes within the same population have on body–scale relation curvilinearity.

TABLE 5.—*Average fork length at time of capture and calculated length at end of each year of life for pygmy whitefish collected in Brooks Lake during summer and fall 1962*

Age group	Sex	Fish in sample	Fork length at capture	Calculated fork length at end of year of life		
				1	2	3
		Number	*Mm.*	*Mm.*	*Mm.*	*Mm.*
I	Male	80	57.2	42.4		
	Female	70	57.2	42.4		
II	Male	32	63.9	41.0	61.3	
	Female	134	69.6	41.7	65.2	
III	Male	2	70.5	41.9	66.1	68.9
	Female	12	74.5	35.6	64.2	71.3
Grand average	Male			42.0	61.6	68.9
	Female			41.6	65.1	71.3
Average increment	Male			42.0	19.6	7.3
	Female			41.6	23.5	6.2
Number of fish	Male	114		114	34	2
	Female	216		216	146	12

TABLE 6.—*Average fork length at time of capture and calculated length at end of each year of life for pygmy whitefish collected in South Bay during summer and fall 1962*

Age group	Sex	Fish in sample	Fork length at capture	Calculated fork length at end of year of life				
				1	2	3	4	5
		No.	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*
I	Male	161	77.0	61.5				
	Female	175	76.2	60.6				
II	Male	214	108.6	62.8	100.7			
	Female	181	112.4	64.7	103.3			
III	Male	14	117.6	65.0	98.9	114.1		
	Female	16	127.1	64.1	99.6	116.2		
IV	Male	4	132.5	64.0	103.3	116.6	119.9	
	Female	12	138.2	64.2	103.8	118.0	129.1	
V	Male	0						
	Female	2	155.0	59.0	82.4	117.5	125.7	135.8
Grand average.	Male			62.4	100.6	114.6	119.9	
	Female			62.8	102.8	117.0	128.6	135.8
Average increment.	Male			62.4	38.2	14.0	5.3	
	Female			62.8	40.0	14.2	11.6	7.2
Number of fish.	Male	393		393	232	18	4	
	Female	386		386	211	30	14	2

The annual growth of female pygmy whitefish from Lake Superior (Keweenaw and Siskiwit Bays), Mich., and Bull Lake and Lake McDonald, Mont., when compared with growth of females from Brooks Lake and South Bay (fig. 6), revealed that the slow growth in Brooks Lake was similar to that in Lake Superior, while growth in South Bay was intermediate between growth in Bull Lake and Lake McDonald. Comparisons of annual growth rates of female pygmy whitefish from the Naknek system with those from MacLure, McLeese, Cluculz, and Tacheeda Lakes (McCart, 1963) indicate (fig. 6) that growth in South Bay was intermediate between growth in McLeese and Cluculz Lakes, while growth in Brooks Lake was slower than in any of the British Columbia lakes. The length attained by pygmy white-

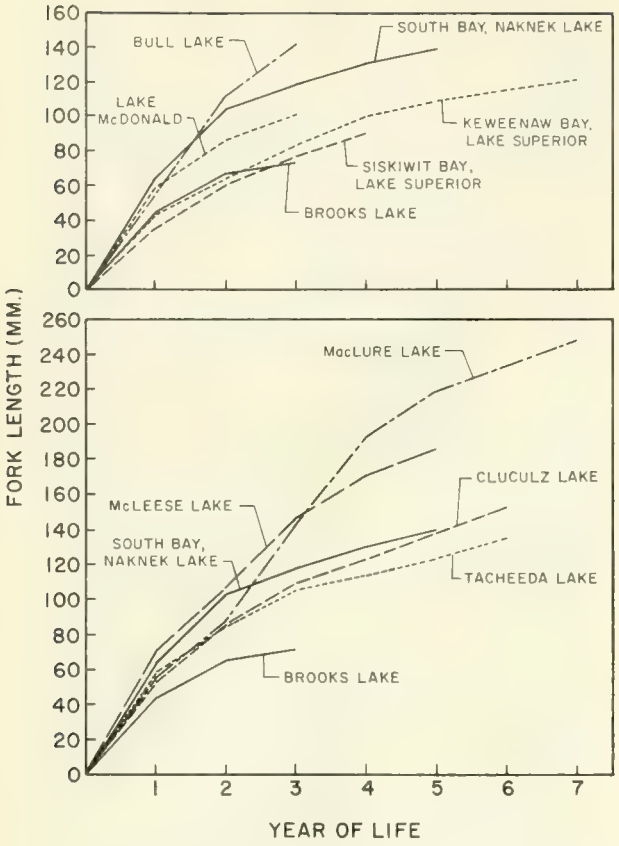

FIGURE 6.—Calculated growth of female pygmy whitefish from Brooks Lake and South Bay, Naknek River system, compared with data from Lake Superior, Mich., and Lake McDonald and Bull Lake, Mont., (Eschmeyer and Bailey, 1955) and MacLure, McLeese, Cluculz, and Tacheeda Lakes, British Columbia (McCart, 1963). Data from Eschmeyer and Bailey were converted from total to fork length.

fish in MacLure Lake is by far the greatest known for this species.

EMPIRICAL GROWTH

Although the average annual growth was not calculated for all lakes in the Naknek system, length frequency distributions of collections from six areas (table 7) provide a basis for growth comparison. The broad range of length frequencies suggests differences in growth rates that reflect the ecological differences in various lakes and basins in the system. The oldest pygmy whitefish collected from Grosvenor Lake, Hammersly Lake, and North Arm were age III+ females 95, 96, and 100 mm.[4] long, suggesting growth rates intermediate between those from Brooks Lake and South Bay. In Iliuk Arm the length of the largest pygmy whitefish, a 132-mm. age IV+ female, is comparable with the average calculated length of the same age fish in South Bay.

The striking difference in growth of pygmy whitefish in Brooks Lake and South Bay is apparent during the first summer. The earliest collections of age 0+ pygmy whitefish were made there in late June and early July. In early July, age 0+ pygmy whitefish were about equal in length in the two areas, averaging between 20 and 23 mm. long. By late August, however, age 0+ pygmy whitefish from South Bay were almost 10 mm. longer than fish from Brooks Lake (fig. 7). Based on the average calculated growth rates, South Bay pygmy whitefish are about 20 mm. longer than Brooks Lake fish at the end of the first growing season (fig. 6). There was little difference in the lengths of age 0+ fish taken in mid-July from Brooks River, North Arm, South Bay, and Brooks Lake. A sample of age 0+ pygmy whitefish from Grosvenor Lake in mid-August indicated an average length similar to that in Brooks Lake in mid-August.

An interesting comparison of the first year growth of pygmy whitefish with that of its close relative, round whitefish (fig. 8), indicates that age 0+ samples of both species collected in the same seine haul from Brooks Lake on August 10, 1962, had no overlap in lengths and round whitefish were considerably larger.

FOOD HABITS

Stomach contents were examined from 62 age 0+ and 396 age I+ and older pygmy whitefish. The age 0+ fish were from South Bay and Brooks and Grosvenor Lakes, while the older fish were from Brooks, Grosvenor, and Hammersly Lakes, South Bay, North Arm, Iliuk Arm, and Brooks River. These fish were collected with seines, otter trawls, and gill nets.

DIET OF AGE I+ AND OLDER FISH

Insects and zooplankton were the two principal groups of food in the diet of age I+ and older pygmy whitefish in the Naknek system (table 8). The relative importance of these two foods varied greatly between lakes. Dipteran insects dominated

[4] Two larger females, 102 and 115 mm. long were collected in North Arm with gill nets on Aug. 9, 1962. Both specimens were mutilated, however, and no scales were available for aging.

the South Bay and Iliuk Arm samples, while crustacean zooplankton dominated samples from Brooks Lake. Stomach samples from Brooks River fish contained predominantly insects, while samples from North Arm and Hammersly and Grosvenor Lakes fish contained about equal amounts of insects and zooplankton.

Larvae, pupae, and adult dipteran and plecopteran nymphs were the main insects eaten by Naknek system pygmy whitefish. Dipteran larvae and pupae (chiefly Chironomidae) accounted for 68, 50, 33, and 88 percent of the food volume from the four South Bay collections (table 8). Forty-seven percent of the volume of stomachs examined from Iliuk Arm consisted of dipteran adults. In all other samples, adult insects accounted for 5 percent or less of the volume. Plecopteran nymphs were the second most important insects eaten, accounting for 32 percent of the volume from a South Bay sample and 40 percent from a Brooks River sample. Five additional orders of insects were occasionally eaten by pygmy whitefish, but these never accounted for more than 5 percent of the volume of any sample.

The principal crustacean foods eaten were the cladocerans *Daphnia*, *Bosmina*, and *Holopedium* and the copepods *Cyclops* and *Diaptomus* (table 8). The crustacean percentage of total volume varied from a trace (South Bay, August 24, 1962) to 100 percent (Brooks Lake, November 7, 1962). Ostracods and amphipods, which were the principal foods eaten by pygmy whitefish in Lake Superior (Eschmeyer and Bailey, 1955), were minor items in the diet of Naknek system fish, occurring in only 8 of 13 samples and never accounting for more than 6 percent of the sample volume.

TABLE 7.—*Length frequencies of pygmy whitefish age I+ and older collected from various areas in the Naknek system, 1961–63*

[M represents males; F, females; C, sexes combined]

Fork length in mm.	Brooks Lake								Grosvenor Lake				Hammersly Lake		
	Aug. 7, 1961		Sept. 14, 1961		June 29, 1962		July 10, 1962	Total	Aug. 5, 1962		Aug. 19, 1963	Total	Aug. 20, 1963		Total
	M	F	M	F	M	F	C		M	F	C		M	F	
26–28															
29–31															
32–34															
35–37															
38–40							1	1							
41–43							6	6							
44–46					9		23	32		1		1			
47–49	4	1	1		28	15	67	116		2		2			
50–52	9	9		2	68	64	254	406	2	4	1	7			
53–55	22	14	3	2	44	49	361	495	3	10	1	14			
56–58	15	14	6	4	5	3	276	323	1	5	7	13			
59–61	8	9	3	6	14	4	79	123	1	3	12	16			
62–64	1	7	3	5	14	11	111	152		2	10	12	1		1
65–67	1	5	1	4	8	13	114	146		3	3	6		1	1
68–70		3		3		8	102	116		3	6	9	1		1
71–73		3		2		6	97	108		2	10	12	2	2	4
74–76		1				1	54	56		10	9	19		2	2
77–79						1	18	19			4	4			
80–82							4	4		1	3	4		1	1
83–85											3	3		1	1
86–88											2	2			
89–91										1	2	3			
92–94											1	1			
95–97											1	1		1	1
98–100															
101–103															
104–106															
107–109															
110–112															
113–115															
116–118															
119–121															
122–124															
125–127															
128–130															
131–133															
134–136															
137–139															
140–142															
143–145															
146–148															
149–151															
152–154															

TABLE 7.—*Length frequencies of pygmy whitefish age I+ and older collected from various areas in the Naknek system, 1961–63*—Continued

Fork Length in mm.	North Arm			Iliuk Arm					South Bay				
	July 21–Aug. 9, 1962		Total	Aug. 2, 1962		July 9, 1963	July 27, 1963	Total	July 22, 1962		Aug. 4, 1962		Total
	M	F		M	F	C	C		M	F	M	F	
26–28													
29–31													
32–34													
35–37													
38–40													
41–43													
44–46													
47–49													
50–52										1			1
53–55					1	1		2					
56–58						1		1					
59–61						4		4		1			1
62–64						5		5		1	2	7	10
65–67				1		4		5	1	4	12	13	30
68–70						5		5	6	3	23	56	88
71–73							3	3	13	14	95	107	229
74–76						2	1	3	11	12	174	244	441
77–79	3		3				2	2	14	8	193	229	444
80–82							2	2	2	6	124	145	277
83–85		3	3								52	45	97
86–88		4	4								10	9	19
89–91		7	7								2	1	3
92–94		5	5										
95–97		6	6			1		1				3	3
98–100		3	3		1			1			6	3	9
101–103		1	1		1		1	2	1	1	17	7	26
104–106									5		49	10	64
107–109						1	1	2	4	5	44	23	76
110–112									14	5	40	37	96
113–115		1	1				1	1	8	6	19	41	74
116–118									7	3	9	26	45
119–121						1		1	6	5	4	13	28
122–124					1			1	1	2	2	6	11
125–127										1	1	4	6
128–130						1	1	2	2	1	2	2	7
131–133						1	1	2	2	3		2	7
134–136										1		2	3
137–139										1		1	2
140–142										1		1	2
143–145													
146–148												2	2
149–151												2	2
152–154													

Other invertebrates found in the diet were pelecypods, nematodes, and arachnids (table 8). Only pelecypods, which accounted for from 5 to 13 percent in samples from North Arm and Brooks and Grosvenor Lakes, were of more than minor importance.

Periphyton (diatoms and other algae), which were present in one Brooks Lake sample and two Brooks River samples, never accounted for more than 4 percent by volume of any sample (table 8).

Fish eggs occurred in both of the Brooks River samples and in the November South Bay samples, amounting to 3, 14, and 38 percent of the volume of food (table 8). Although the eggs were partially digested in some stomachs and could not be identified, they all appeared to be salmon eggs. Large numbers of adult sockeye salmon spawn in Brooks River during the summer and early fall. Even after spawning is completed in the fall there is a frequent drift of dislodged eggs out of Brooks River into South Bay. Kendall (1921) found salmonid eggs in stomachs of pygmy whitefish collected from Lake Aleknagik in August, and Eschmeyer and Bailey (1955) found whitefish eggs in stomachs of pygmy whitefish collected from Lake Superior in January. Eschmeyer and Bailey speculate that fish eggs, when available, may be an important item in the diet of the pygmy whitefish.

Sand grains accounted for 29 percent of the volume in the Grosvenor Lake sample and represented from 6 to 10 percent of the volume in four additional samples (table 8). Only two samples, both from Brooks Lake and containing principally zooplankton, were entirely devoid of sand grains. Occasionally fish were found with more than 100 sand grains in their stomachs. Eschmeyer and Bailey (1955) found sand grains in 9 percent of the Lake Superior fish examined.

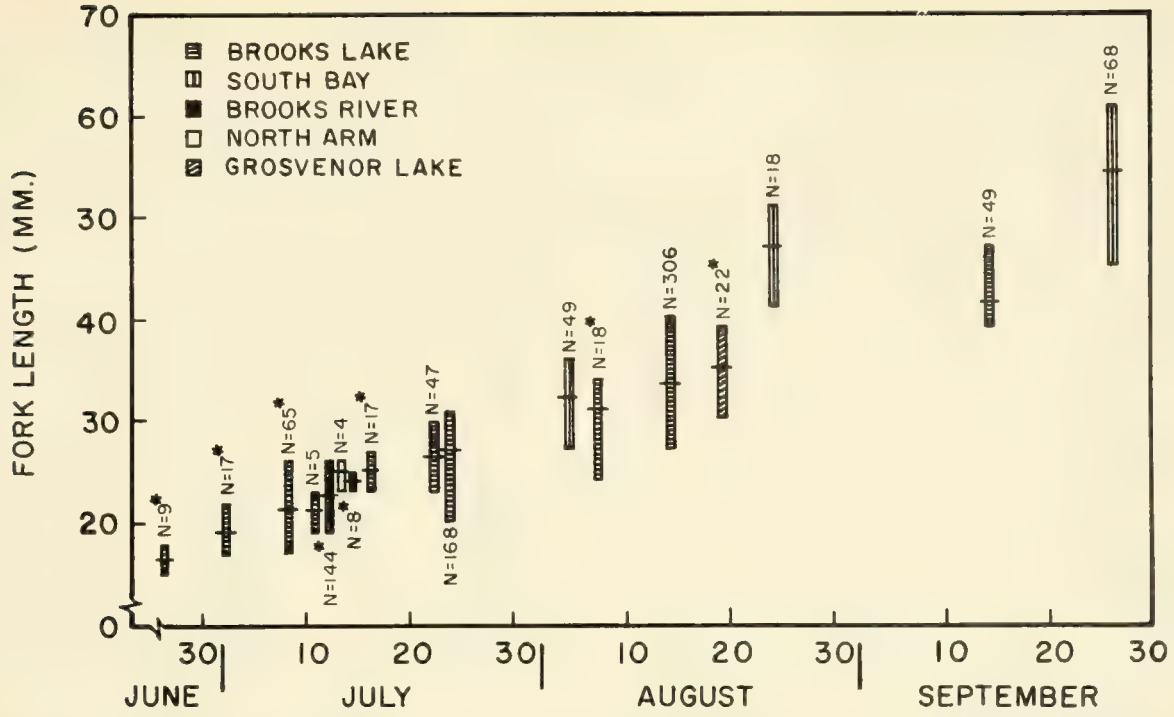

FIGURE 7.—Length frequencies of age 0+ pygmy whitefish collected in 1962 and 1963. Vertical bar represents length range; horizontal line represents mean length of each collection. Asterisk indicates collection was made in 1963.

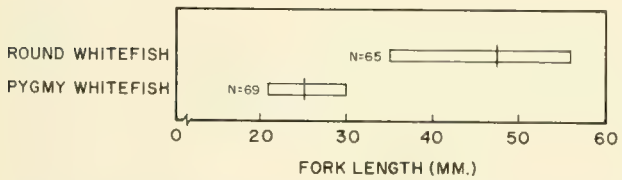

FIGURE 8.—Range and mean length of age 0+ round whitefish and pygmy whitefish caught in the same seine haul in Brooks Lake, August 10, 1962. Horizontal bar shows range; vertical bar indicates mean length of samples.

Plant debris such as small twigs, bits of wood, grass, seeds, and spruce needles occurred in nine samples and accounted for 14 percent of the volume in both samples from Brooks River (table 8). The relatively high occurrence of these items in Brooks River probably represents drift items.

The significance of fish scales in six samples (table 8) is not understood. All undigested scales that could be identified were from pygmy whitefish. No fish remains other than scales were found in any stomachs. Our observations suggest that pygmy whitefish might readily ingest any small bright object either in the current or from the stream or lake bottom.

Underwater observations of pygmy whitefish feeding in lower Brooks River showed that they frequently picked up mouthfuls of material off the bottom and passed fine silt, sand grains, and bits of debris posteriorly through their gill openings. They did not feed along the bottom in a suckerlike manner, but made short distinct jabs or darts, apparently at specific food items, such as insect larvae, when picking up mouthfuls of bottom material. Sand grains and other bits of debris are undoubtedly passed into the alimentary tract during such feeding behavior. Not all pygmy whitefish feeding activity in Brooks River was associated with the bottom. Frequently individual fish would rise off the bottom, as much as 35 to 50 cm. in water 1 m. deep and would pick specific items out of the passing current. With the diet of pygmy whitefish being primarily zooplankton and insects in various parts of the Naknek system and macrobenthic crustaceans in Lake Superior (Eschmeyer and Bailey, 1955), it is obvious that the species has a flexible diet and feeding behavior.

TABLE 8.—*Percentage of total volume [1] of different food items in stomachs and (in parentheses) percent frequency occurrence [2] for 13 samples of age I+ and older pygmy whitefish taken with seines, gill nets, and otter trawls from various parts of the Naknek system*

[T represents Trace]

Food item	South Bay				Brooks River		Iliuk Arm	North Arm	Grosvenor Lake	Hammersly Lake	Brooks Lake		
	Aug. 4, 1962, Seine	Aug. 24, 1962, Seine	Nov. 9 1962, Seine	Apr. 16, 1963, Gill net	July 28, 1963, Seine	Aug. 24–25, 1963, Trawl	July 9, 1963, Seine	July 22–Aug. 9, 1962, Gill net	Aug. 19, 1963, Trawl	Aug. 17–20, 1962, Gill net	July 10, 1962, Trawl	Nov. 7, 1962, Trawl	July 22–26, 1962, Trawl
Insects:	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*
Dipteran:													
Larvae	49 (67)	9 (70)	33 (50)	87 (100)	9 (83)	14 (95)	7 (59)	34 (78)	28 (90)	28 (75)	T (25)		15 (57)
Pupae	19 (43)	41 (97)		1 (5)	9 (70)	24 (80)	16 (70)		5 (30)	34 (88)	1 (18)		T (5)
Adults	T (6)				1 (3)	5 (40)	47 (85)						4 (24)
Plecopteran:													
Nymphs	9 (13)	32 (73)			40 (73)	8 (43)	6 (44)						
Tricopteran:													
Larvae	2 (11)					T (10)			T (5)				
Other insects [3]	T (2)					1 (13)	5 (30)						
Crustaceans:													
Cladocerans [4]	4 (15)	T (10)	8 (40)	2 (21)	9 (37)	4 (40)	16 (81)	16 (67)	20 (85)	9 (38)	69 (100)	70 (100)	26 (76)
Copepods [5]	1 (7)	T (3)	4 (10)	2 (21)	7 (23)	5 (43)	2 (30)	27 (89)	14 (65)	27 (62)	29 (95)	30 (94)	44 (100)
Ostracods	T (2)			6 (26)				3 (17)	T (5)	1 (38)	1 (34)		T (5)
Amphipods							T (4)						
Other invertebrates:													
Pelecypods [6]								13 (28)	5 (10)				6 (5)
Nematodes		1 (10)		T (11)	T (10)	1 (32)	T (4)	5 (39)		T (25)			1 (38)
Arachnids		1 (17)				T (3)					T (2)		
Miscellaneous:													
Periphyton [7]					T (10)	4 (35)							4 (10)
Fish eggs			38 (30)		3 (13)	14 (22)							
Sand grains	10 (67)	1 (27)	9 (80)	1 (26)	6 (87)	6 (82)	T (11)	1 (17)	29 (90)	1 (25)			T (10)
Plant debris [8]	2 (17)	1 (20)	8 (30)	1 (21)	14 (60)	14 (70)	T (18)	T (6)					T (5)
Fish scales	3 (22)	15 (40)	T (10)		1 (30)	1 (27)	T (22)						
Number of stomachs examined	60	30	20	20	30	63	27	20	21	9	44	31	21
Percent empty stomachs	10	0	50	5	0	5	0	10	5	11	0	0	0
Length range	68–130	72–113	100–134	80–111	97–136	81–144	56–130	76–100	52–97	68–80	53–80	55–77	55–77
Mean volume of contents [2] (in ml.) per stomach	0.11	0.23	0.13	0.09	0.27	0.46	0.39	0.10	0.18	0.12	0.18	0.17	0.06

[1] Based on aggregate contents of all stomachs in each sample.
[2] Based only on stomachs containing food.
[3] Tricopteran adults, coleopteran adults and larvae, hemipteran, hymenopteran, and collembolan adults.
[4] *Daphnia longiremis, D. rosea, Bosmina coregoni, Holopedium gibberum.*
[5] *Cyclops strenuus* and *Diaptomus gracilis.*
[6] *Pisidium.*
[7] Diatoms and filamentous algae.
[8] Small sticks, bits of wood, seeds, and leaves.

DIET OF AGE 0+ FISH

Crustacean zooplankton was the major food in two samples of age 0+ fish—one from South Bay, July 11, 1963, and one from Brooks Lake, August 14, 1962. Insects and zooplankton were about equal in volume in the September 26, 1962, South Bay and August 19, 1963, Grosvenor Lake samples (fig. 9). It appears that in those areas where insects are heavily utilized by older pygmy whitefish, the diet shift of fish from zooplankton to insects occurs late during the first summer of life. Eschmeyer and Bailey (1955) found copepods to be the dominant food of age 0+ pygmy whitefish from Lake Superior in September.

DIEL VARIATIONS IN DIET

The sample of age I+ and older fish from Brooks River on August 24–25, 1963 (table 8), was collected from the same riffle area at four adjacent 6-hour intervals to determine diel differences in quantity and quality of foods eaten. No significant difference in the composition of diet items was found throughout the 24-hour period; however, the average volume of food material per

stomach was three times as great at midday as at midnight (fig. 10). The most intense feeding period during this 24-hour period apparently was during daylight hours and not during darkness.

COMPARISONS OF GROWTH AND DIET

By comparing the dramatically different growth rates and sizes that pygmy whitefish attain in the Naknek system (figs. 2 and 6) with the differences in diet, a strong positive correlation between size of fish and utilization of insects becomes apparent. An analysis was made by first grouping all contents from each sample into three categories (insects, zooplankton, and other), then grouping the samples according to the relative importance of insects and zooplankton. Three rather distinct groups of samples resulted: one with heavy, one with moderate, and one with almost no insect utilization. These grouped samples compared with the largest known pygmy whitefish from the same grouped areas (fig. 11) illustrate the correlation between insect utilization and size. Maximum size is not the only index, because the general ranges of length frequencies from different parts of the system (table 7) fall into the same groupings. If this correlation is biologically valid, it raises a question as to why Brooks Lake pygmy whitefish do not eat insects. Merrell (1964) has shown that other Brooks Lake fishes utilize insects, which indicates their general availability. No comparative data are available, however, on differences in insect populations in the Naknek system.

Preference for, access to, or utilization of specific foods may not directly account for differences in growth rates of pygmy whitefish populations in Brooks Lake and South Bay-Iliuk Arm. Basic differences in ecological characteristics of the areas such as morphometry, limnology, productivity,

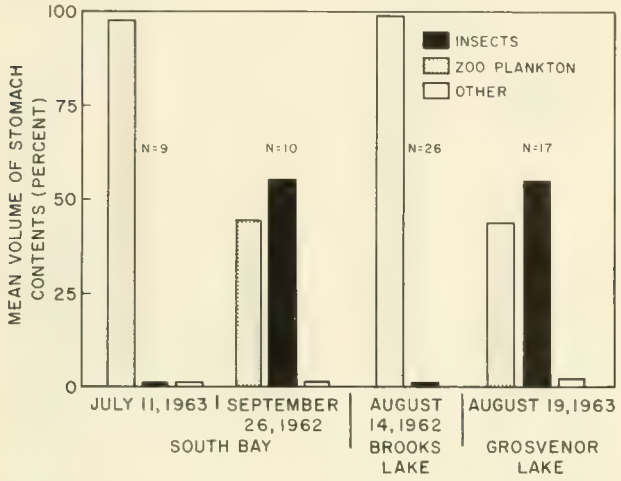

FIGURE 9.—Percent of total volume of stomach contents of age 0+ pygmy whitefish by major food categories.

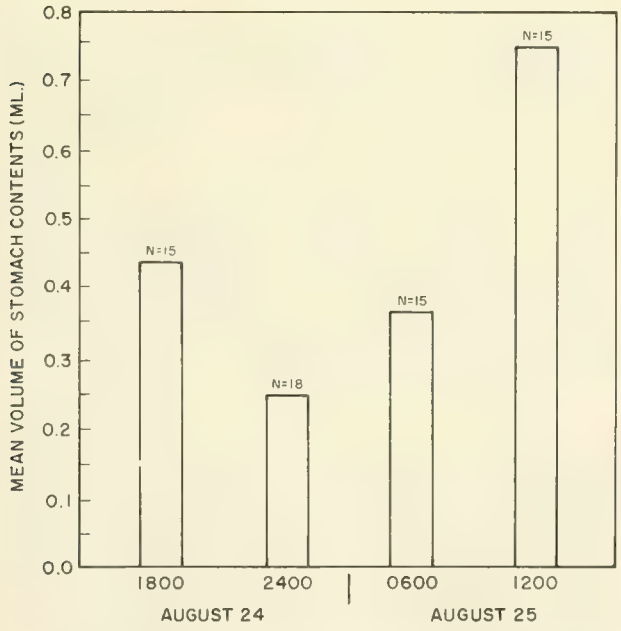

FIGURE 10.—Variation by time of day in mean volumes of stomach contents of 63 pygmy whitefish caught at 6-hour intervals from the same area in Brooks River, August 24 and 25, 1963.

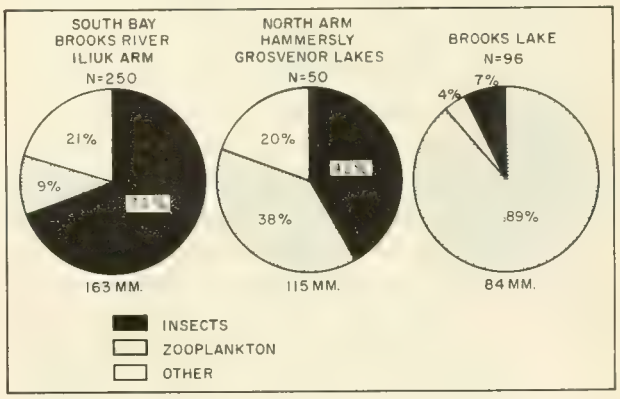

FIGURE 11.—Relative importance of insects, zooplankton, and other foods in diet of pygmy whitefish from three areas of Naknek system. Data based on percent of sample volumes shown in table 8. Number beneath each figure represents largest pygmy whitefish collected from the grouped area.

species combinations of fishes, and food organisms are interwoven in a complex of relations that result in distinctly different environments. Differences in growth rates, longevity, and food habits of pygmy whitefish in the Naknek system probably reflect adaptive responses to these overall environmental differences and not simply the availability or use of certain food items.

The differences we found in *Prosopium coulteri* populations in Brooks Lake and South Bay-Iliuk Arm parallel the differences in *Coregonus peled* (Gmelin) populations in the Swedish lakes Vjomsjon and Uddjaur-Storavan (Lindstrom and Nilsson, 1962). In Sweden, *C. peled* was a slow-growing plankton feeder in Lake Vjomsjon and a fast-growing insect feeder in Lakes Uddjaur-Storavan. As previously discussed, *P. coulteri* is a slow-growing plankton feeder in Brooks Lake and a fast-growing insect feeder in South Bay-Iliuk Arm. Lake Vjomsjon had fewer associated whitefish species, proportionately less littoral area, and probably lower productivity than Lakes Uddjaur-Storavan. In the Naknek system, Brooks Lake has fewer associated whitefish species, less littoral area, and lower productivity than South Bay-Iliuk Arm. The observed plasticity of the genus *Prosopium* in response to environmental differences in the Naknek system is similar to that widely recognized in coregonid and leucichthid whitefishes (Walters, 1955; Svardson, 1957; and others). The variability in meristics and morphology found in pygmy whitefish by McCart (1963) also emphasizes this plasticity in *Prosopium*.

REPRODUCTION

Data on pygmy whitefish reproduction were collected from various areas as follows: sex ratio and age and size at maturity—South Bay and Brooks Lake; fecundity—South Bay, Brooks Lake, and North Arm; and seasonal maturation and spawning behavior—South Bay and Brooks River.

SEX RATIOS

Only a few large samples from Brooks Lake and South Bay were processed for sex ratios, but they revealed nearly equal ratios (table 9). The largest specimens were almost always females (table 7), a phenomenon undoubtedly due to the greater longevity and the faster growth rate of females. These larger females, however, constituted a numerically minor segment of the population. Eschmeyer and Bailey (1955) and McCart (1963) also found females to be the oldest and largest fish in their collections.

TABLE 9.—*Sex ratios of pygmy whitefish, Brooks Lake and South Bay, collected during the summers 1961–62*

Location and date	Number of fish	Sex ratio females to males
Brooks Lake:		
Aug. 7, 1961	127	1:0.92
June 29, 1962	365	1:1.08
South Bay:		
July 23, 1962	182	1:1.13
Aug. 24, 1962	1,907	1:0.82

AGE AND SIZE AT MATURITY

The degree of maturity in age groups I and II varied between lake populations and between sexes within a single population (table 10). In Brooks Lake 10 percent of the females and 36 percent of the males reached sexual maturity during their second growing season (age I+). In South Bay no females and only 2 percent of the males matured as age I+ fish. In both lakes more than 95 percent of the age II+ fish and all of the older fish were mature.

TABLE 10.—*Age at maturity of pygmy whitefish collected during the summer and fall from Brooks Lake and South Bay, 1961–62*

Age	Brooks Lake				South Bay			
	Males		Females		Males		Females	
	Fish in sample	Mature	Fish in sample	Mature	Fish in sample	Mature	Fish in sample	Mature
	Number	*Percent*	*Number*	*Percent*	*Number*	*Percent*	*Number*	*Percent*
I+	67	36	58	10	160	2	175	0
II+	28	96	96	97	214	99	181	97
III+	2	100	11	100	14	100	16	100
IV+	-	-	-	-	4	100	12	100
V+	-	-	-	-	-	-	2	100

In Brooks Lake and South Bay, only a slight tendency exists for males to mature at a smaller size than females. In contrast, Eschmeyer and Bailey (1955) found 100 percent of the males mature at sizes smaller than the smallest mature females. Because of the great differences in growth rates in the Naknek system, there is no overlap in the size at maturity between Brooks Lake and South Bay pygmy whitefish (table 11).

TABLE 11.—*Size at maturity of pygmy whitefish collected during the summer and fall from Brooks Lake and South Bay, 1961–62*

Length groups	Brooks Lake				South Bay			
	Males		Females		Males		Females	
	Fish in sample	Mature	Fish in sample	Mature	Fish in sample	Mature	Fish in sample	Mature
Mm.	*Number*	*Percent*	*Number*	*Percent*	*Number*	*Percent*	*Number*	*Percent*
44–46	10	0						
47–49	35	0	16	0				
50–52	81	0	72	0			1	0
53–55	73	8	71	0				
56–58	28	29	29	3				
59–61	25	76	19	21			1	0
62–64	18	94	24	71	2	0	8	0
65–67	13	100	26	96	13	0	17	0
68–70	3	100	22	100	29	0	59	0
71–73	3	100	36	100	105	0	121	0
74–76			20	100	185	0	256	0
77–79			4	100	207	0	237	0
80–82			2	100	126	2	151	0
83–85					42	5	45	2
86–88					10	20	9	11
89–91					1	0		
92–94								
95–97							3	67
98–100					6	100	2	100
101–103					18	94	8	100
104–106					54	100	10	100
107–109					48	98	28	90
110–112					54	100	42	98
113–115					27	100	47	98
116–118					15	100	29	100
119–121					10	100	18	100
122–124					3	100	8	100
125–127					1	100	5	100
128–130					4	100	3	100
131–133					2	100	6	100
134–136					2	100	5	100
137–139							4	100
140–142							3	100
143–145								
146–148							5	100
161–163							1	100

FECUNDITY

The total number of maturing eggs in pygmy whitefish ovaries were counted for 59 fish from South Bay, 19 from Brooks Lake, and 7 from North Arm. The number of eggs ranged from 103 to 1,153 per female. Body length-fecundity equations computed for each sample showed some difference between areas. However, a single equation was determined (fig. 12) by grouping all 85 females, because there was no overlap in the size range of females between samples.

The salient features of these fecundity data are (1) that a broad range of fecundities exists in different parts of the system and (2) that pygmy whitefish from the Naknek system are considerably more fecund than the same size fish from Lake Superior. We transformed the total length-fecundity relation given by Eschmeyer and Bailey (1955) into a fork length-fecundity relation for comparison with our data. A 120-mm. female

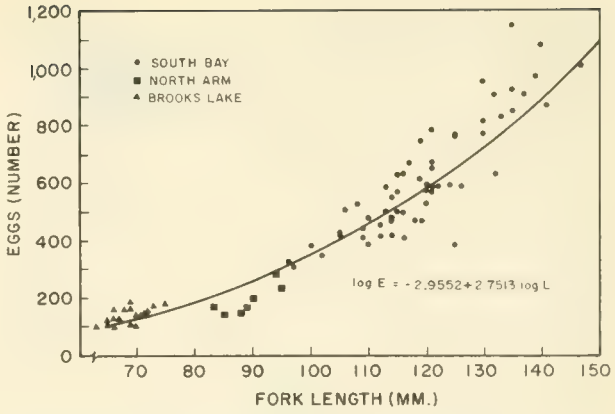

FIGURE 12.—Length-fecundity relation of pygmy whitefish from three areas of Naknek system. Equation derived by combining data from the three areas.

from Lake Superior (130 mm. total length) averaged about 440 eggs, while the same size female from the Naknek system averaged about 580 eggs. These differences in fecundity could be adaptive responses of the various populations to different environmental conditions that produce higher or lower survival opportunities for the species (Svardson, 1949; Nikolsky, 1963).

SPAWNING SEASON AND BEHAVIOR

Egg size in maturing females from South Bay in 1962 increased markedly between late summer and the fall spawning period. Egg diameters that averaged 1.1 mm. in early August increased to 2.4 mm. in ripe females in early November, while ovary weight increased from 3.5 to 16.5 percent of the total body weight (fig. 13). Egg size and ovary weight relative to body weight in near ripe fish from Lake Superior (Eschmeyer and Bailey, 1955) were 2.0 mm. and 15 percent.

Spawning of pygmy whitefish in Brooks Lake and South Bay in 1962 and 1963 apparently occurred between mid-November and mid-December. Mature, ripe males and females from South Bay were collected near the mouth of Brooks River on November 7 and 9, 1962. The water temperature in South Bay on November 9, 1962, was 3.9° C. Both eggs and sperm could easily be extruded by exerting slight pressure on the abdomen, and females as well as males were tuberculate over much of the body. The ventral fins of both sexes were orange. Pygmy whitefish from Brooks Lake on November 7, 1962, were not quite

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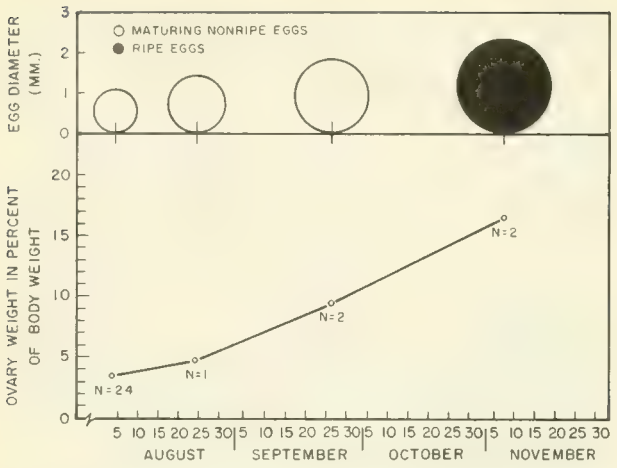

FIGURE 13. Seasonal maturation of pygmy whitefish collected from South Bay, 1962. Average egg diameter based on minimum of 10 eggs per female. N equals number of females examined.

as ripe as those from South Bay. Although mature fish taken in South Bay on October 29 and November 5, 1963, were not quite ripe, three specimens taken from Brooks River on the night of November 6 apparently were, because sex products could be readily extruded from them.

The spawning period in the Naknek system agrees with most other spawning information on pygmy whitefish. The time of spawning in Lake Superior (Eschmeyer and Bailey, 1955), Glacier National Park, Mont. (Schultz, 1941), and four British Columbia lakes (McCart, 1963) was believed to be in November or December. The November–December spawing in the Naknek system compares closely with the supposed time of spawning in Lake Superior and Glacier National Park, Mont. (Eschmeyer and Bailey, 1955; and Schultz, 1941). Weisel and Dillon (1954) collected sexually mature and spent pygmy whitefish from Bull Lake between December 26 and January 12. Kendall (1917 and 1921) reported on six pygmy whitefish collected from the Chignik River system, Alaska, about November 1, 1912. These fish (Kendall, 1921) were "mature individuals ready to spawn," which agrees with the other known spawning times of this species.

Exceptions to the late fall and winter spawning of pygmy whitefish have been noted. Kendall (1921) reported that some pygmy whitefish collected on July 20, 1909, and August 2, 1912, from the outlet of Lake Aleknagik were in breeding condition. Apparently the collector of one of these samples reported that pygmy whitefish were passing out of Lake Aleknagik in large numbers, and Kendall interpreted this as a spawning run. We question the validity of this interpretation and doubt that a spawning migration was occurring as early as July 20 or August 2, although individual specimens might have seemed ready to spawn. McCart (1963) found a physiologically atypical female in Cluculz Lake, British Columbia, on July 15, 1962, which appeared to be ripe. We examined pygmy whitefish collected on July 13, 1963, from Wood River just below the outlet of Lake Aleknagik by Dr. R. L. Burgner of the Fisheries Research Institute, University of Washington, and found the condition of the gonads to be 3 or 4 months from full maturity. Two of the Wood River females had average egg diameters of 1.0 mm., and the ovaries made up only 2.7 percent of the body weight (fig. 13). Burgner (personal communication) reports that large numbers of pygmy whitefish can be seen throughout much of the summer in Wood River below Lake Aleknagik. These observations and Kendall's (1921) comments on fish passing out of the lake could represent the seasonal feeding movements of a lake population similar to that observed during the summer in South Bay and lower Brooks River. Pygmy whitefish may spawn below Lake Aleknagik, but probably later than Kendall believed.

Although specific details of spawning behavior were not observed, we determined that pygmy whitefish (in Brooks River at least) spawn only at night, as do mountain whitefish in Montana (Brown, 1952). Routine underwater surveys in early November in 1962 and 1963 revealed no pygmy whitefish in Brooks River during daylight hours, although large numbers of ripe or nearly ripe fish were known to be in South Bay off the river mouth. On a dive just after dusk on November 5, 1963, divers using underwater hand lamps observed that a few large pygmy whitefish had moved into lower Brooks River from South Bay. Between 20 and 25 pygmy whitefish were observed in the same area the following night about 3 hours after darkness. These fish probably represented the beginning of the spawning run in 1963.

South Bay fish probably remain in the lake in the vicinity of Brooks River until they reach full maturity, when they move into the river at night

to spawn. Periodic observations along the streambank at night with a lantern in late November and early December in 1963 continued to reveal the presence of pygmy whitefish in the stream. Unseasonably cold temperature, however, caused ice conditions that precluded intensive observations. About 100 fish were seen just at the mouth of Brooks River during a night dive on December 16, 1963. Most of these fish were individually scattered over the stream bottom, although one congregation of 8 to 10 fish may have represented a spawning group. These particular fish darted wildly about upon encountering the underwater spotlight. The water temperature in Brooks River on December 16 was 0.3° C. All adult pygmy whitefish taken in gill nets under ice in South Bay near the river mouth on December 12 and 18 were spent.

DISCUSSION

In the Naknek River system pygmy whitefish apparently reach their greatest density in Brooks Lake where they may be the most abundant species in the lake. These conclusions are based on the combined numbers of each species caught in all sampling gears from 1961 to 1963. In Brooks Lake, South Bay, and Iliuk Arm, pygmy whitefish are commonly associated with juvenile sockeye salmon. This relation merits consideration because of the commercial value of the Naknek River system sockeye salmon.

Although the association of two species predetermines some sort of interspecific relation, in fishes it is usually difficult to determine the exact nature of this relation. Larkin (1956), who considered competition in a concise limited sense, points out that competition itself is difficult to separate from other complex interrelations between fish species. Rogers (1961), after carefully considering the diets of young-of-the-year sockeye salmon and three age groups of threespine sticklebacks collected from similar ecological areas of Wood River Lakes, could only conclude that "potential food competition exists." Greenbank and Nelson (1959), in studying the threespine stickleback in Karluk Lake, conclude that "Quantitative information is insufficient to assess accurately the benefit or harm to salmon production caused by the stickleback population." Johnannes and Larkin (1961) could demonstrate severe competition between redside shiners (*Richardsonius balteatus*) and rainbow trout for amphipods in Paul Lake, British Columbia, only because of long-term data that included preshiner amphipod densities along with feeding habits and growth rates of the trout.

In the present study it is impossible on the basis of existing data to demonstrate direct interspecific competition in any form between pygmy whitefish and juvenile sockeye salmon or other whitefishes. It is possible, however, that the combined effects of interspecific and intraspecific relations of these species may influence the growth and general well-being of each in various parts of the Naknek system. Although McCart (1963) could not demonstrate direct competition between pygmy whitefish and other whitefishes, he found indications of interactive segregation between whitefishes which resulted in differences in depth distribution and growth rates. He also noted that the large MacLure and McLeese Lake pygmy whitefish were the only ones in British Columbia that did not coexist with another species of the genus *Prosopium*. In the present study the largest pygmy whitefish were found in South Bay and Iliuk Arm where three other whitefishes occur (round and humpback whitefish and least cisco), while the smallest pygmy whitefish were found in Brooks Lake where round whitefish is the only other whitefish. Although growth rates of pygmy whitefish in the Naknek system are correlated with different diets, McCart (1963) found no differences in diets of this fish in four lakes where growth was quite different.

Both pygmy whitefish and juvenile sockeye salmon feed heavily on zooplankton in Brooks Lake, although Merrell (1964) points out that during late spring and early summer, insects may be the most important item in the diet of Brooks Lake sockeye salmon (age I+ and older). Even though differences in the production of sockeye salmon smolts in Brooks Lake have varied from 60,000 to 360,000 during recent years, there has been little difference in the mean size of age I+ smolts. This suggests that densities of young salmon, together with other environmental influences such as potentially competitive dense populations of pygmy whitefish, have not altered the basic growth rate of sockeye salmon in Brooks Lake.

Interspecific association of juvenile sockeye salmon and pygmy whitefish in South Bay and Iliuk

Arm is complicated by several factors. First, a greater number of other associated species occur in these areas than in Brooks Lake. Second, in addition to serving as primary rearing areas for salmon produced in adjacent spawning areas such as Brooks River and Margot Creek (a tributary of Iliuk Arm), both South Bay and Iliuk Arm, of necessity, serve as migration lanes for salmon produced in upsystem areas. This point is further complicated by interlake movement whereby some juvenile sockeye salmon begin their nursery lake existence in upstream lakes (i.e. Coville and Brooks), then migrate into downstream nursery areas (i.e. Iliuk Arm and South Bay) to complete their first year of life.[5] Thus, the juvenile sockeye salmon populations in South Bay and Iliuk Arm are frequently undergoing dramatic changes in density apart from normal fluctuations in the local population. Although pygmy whitefish feed primarily on insects in South Bay and Iliuk Arm, the diet of young sockeye salmon in these areas is not known. It may be that no possible food competition exists between these species in South Bay and Iliuk Arm.

The reasons for the marked differences in the biology of pygmy whitefish populations in Brooks Lake and South Bay are poorly understood. Pygmy whitefish in Brooks Lake grow slower, mature earlier, and live shorter lives than those in South Bay or Iliuk Arm. Consequently, spawning females are younger, significantly smaller, and less fecund in Brooks Lake. Yet, the species is extremely successful in Brooks Lake, as evidenced by abundance. Factors contributing to this success undoubtedly deal with lower mortalities from fertilized egg to maturity. Because of early maturity, short life span, and small size, pygmy whitefish in Brooks Lake fit the concept of a "dwarfed or small form" discussed by Svardson (1957), Alm (1959), and Fenderson (1964). As pointed out by Alm, a "dwarfed form" with short life and early maturity is distinct from a slow-growing "normal form" which has greater longevity and matures at an older age but still at a small size. Dwarfism may provide a species with advantages in survival and competition (Lindstrom and Nilsson, 1962; McCart, 1963; and Fenderson, 1964).

On the basis of recent data from Lake Aleknagik and Chignik Lake, Peter J. McCart (personal communication) believes that two distinct sub-populations of pygmy whitefish may occur sympatrically in these lakes. One form, which is generally larger, is a river-oriented insect feeder with low gill raker counts and is apparently confined to shallow water. The other form is a lake-oriented plankton feeder with high gill raker counts and inhabits deep water. These criteria, in part, apply to some of the differences found in populations in the Naknek system. This is particularly true with the insect feeders in South Bay where the population is strongly oriented to Brooks River and the relatively shallow waters of South Bay. In other parts of the system, however, differences in ecological distribution represent exceptions to this general scheme. In Iliuk Arm, large fast-growing insect feeders occur from shallow beaches to maximum depths of 168 m., whereas in Brooks Lake, slow-growing insect feeders occur from the shallow to the deepest depths. Although we have not studied meristic variation of populations of pygmy whitefish in the Naknek system in detail, the insect feeders in South Bay and Brooks River have lower gill raker counts than the plankton feeders in Brooks Lake. Eschmeyer and Bailey (1954, p. 174) point out that gill rakers from pygmy whitefish in rivers, or lakes dominated by rivers, tend to be fewer in number and shorter in length than those from lacustrine environments. Whether differences found in populations of pygmy whitefish in the Naknek system represent genetically distinct subpopulations or the adaptive responses of the species in utilizing the many environments present in the system cannot be determined without additional study.

Differences in diet in various parts of the system have been discussed and correlated with growth rates. Actually, growth rates are correlated not only with the degree of insect utilization but also with the rate of phytoplankton productivity in various areas. Primary productivity is relatively high in South Bay and Iliuk Arm, low in Brooks Lake, and intermediate in North Arm and Grosvenor Lake.[6] A notable exception to correlating growth rates of pygmy whitefish with primary

[5] Summary report of studies on the optimum escapement of sockeye salmon in southwestern Alaska, 1961–62. Prepared by the Bureau of Commercial Fisheries Biological Laboratory, Auke Bay, Alaska, and Fisheries Research Institute, University of Washington, Seattle. (Manuscript on file at the BCF Laboratory.)

[6] See footnote 2 on p. 557.

productivity is that Coville Lake, which has the shallowest mean depth, the highest water temperatures, and the highest primary productivity in the system, apparently has only a small population of intermediate size pygmy whitefish; however, Coville Lake may have denser populations of other species (i.e. pond smelt, humpback whitefish, and juvenile sockeye salmon) than other parts of the system.

Until comparative data are available on the relative abundance of various food groups and the diets of associated fishes in different areas, it is impossible to determine the role of food availability or preference for specific foods in evaluating differences in the biology of pygmy whitefish in the Naknek system. Rather than simple differences in diet, growth, or ecological distribution, we feel the dramatic differences found in pygmy whitefish populations in the Naknek system probably reflect widely varying adaptive responses of a highly plastic species to the complex of environmental differences found throughout the system.

SUMMARY

The pygmy whitefish has the greatest discontinuous distribution of any fresh-water fish in North America, occurring in the Atlantic, Pacific, and Arctic Ocean drainages. It is widely distributed and locally abundant in lakes of the Naknek River System in southwest Alaska.

More than 10,000 pygmy whitefish were collected from the Naknek system with seines, otter trawls, tow nets, and gill nets from 1961 to 1963. This species seems to have a prominent role in the dynamics of some Naknek system fish populations.

In the Naknek system, pygmy whitefish occur in all benthic areas from shallow littoral depths to the deepest areas available. Seasonally, in certain age groups and in certain areas, they occur in limnetic waters of lakes and in streams.

Nineteen species, including the closely related round whitefish, occurred in catches with pygmy whitefish in various parts of the Naknek system.

Polynomial equations were used to express the curvilinear relation between body length and anterior scale radius. Body length at scale formation is about 25 mm.

The oldest and largest fish from the two areas studied most intensively was an age V 163-mm. female from South Bay and an age III 84-mm. female from Brooks Lake. Length frequency distributions from other areas were intermediate between these extremes. Calculated and observed growth indicated that growth was much greater in South Bay than in Brooks Lake. Both sexes in Brooks Lake showed a tendency to mature at an earlier age than in South Bay.

Dipteran insects were the principal foods eaten by pygmy whitefish in South Bay. Crustacean plankton dominated their diet in Brooks Lake. In other areas insect and zooplankton foods were about equal in importance. In areas where insects were important in the diet of older fish, the shift from zooplankton to insect foods in age 0+ fish began during the first summer of life. A positive correlation between growth and insect utilization was found.

The fork length–fecundity relation of Naknek system pygmy whitefish is expressed by the equation

$$\text{Log } E = -2.9552 + 2.7513 \log L.$$

where E equals number of eggs per female and L equals fork length of the fish. Fecundity in Naknek system fish exceeds that in Lake Superior fish.

Spawning occurs in November and December. South Bay fish move into Brooks River for spawning only at night. Eggs in ripe fish from South Bay averaged 2.4 mm. in diameter, and the ovaries were 16.5 percent of the body weight.

Potential interspecific competition exists between pygmy whitefish and juvenile sockeye salmon, particularly in Brooks Lake where foods are similar and the whitefish are numerous.

Slow growth, low fecundity, and short life characterize Brooks Lake pygmy whitefish. These factors must be compensated for by lower mortality from fertilized egg to maturity than in the South Bay population, which is characterized by fast growth, higher fecundity, and longer life.

The wide range in growth rate, fecundity, longevity, and diet of populations of pygmy whitefish in the Naknek system is probably due to the adaptive responses of a highly plastic species to the variety of environmental characteristics, such as water quality and clarity, drainage geology, phytoplankton productivity, lake morphometry, fish species, and food organism associations found in different parts of the system.

ACKNOWLEDGMENTS

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A REVIEW OF WESTERN ATLANTIC CAT SHARKS, SCYLIORHINIDAE, WITH DESCRIPTIONS OF A NEW GENUS AND FIVE NEW SPECIES

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ABSTRACT

A new genus *Schroederichthys* is described, together with its type species *Schroederichthys maculatus* from the western Caribbean and a second species *Schroederichthys tenuis* from the Atlantic off Brazil. *Scyliorhinus meadi* from the east coast of Florida, *Scyliorhinus hesperius* from the western Caribbean, and *Galeus cadenati* from the vicinity of Panama are also described. All 15 of the known western Atlantic species are illustrated, and species characters thought to be of value for revisionary studies are noted.

The purpose of this paper is to review the western Atlantic cat sharks with especial attention to description of those characteristics of genera and species that are of interest for a revision of the cat sharks of the world; and also to describe new material collected by exploratory fishing vessels of the Bureau of Commercial Fisheries in the western Atlantic, including representatives of a new genus and five new species.

For a revision of the family, more material should be examined than is now available in American museum collections. The distinctions between the genera *Scyliorhinus* and *Halaelurus*, for example, appear to be somewhat superficial, but a revision of generic arrangement is impractical without a survey of all known species and the use of a greater number of diagnostic characters than can be gleaned from the terse and noninformative descriptions of many of the nominal species. A family revision which is in progress will provide a better opportunity for treatment of genera.

SOURCES OF MATERIAL

Collections of cat sharks made by the Bureau of Commercial Fisheries exploratory fishing vessels, *Oregon*, *Silver Bay*, and *Combat*, are the principal source of material for this report. Studies of these collections were supplemented by examination of the relatively small numbers of cat sharks in the U.S. National Museum, the Museum of Comparative Zoology at Harvard College, and the Natural History Museum of Stanford University. An important series of *Apristurus* in the Museum of Comparative Zoology collected by the *Cap'n Bill II*, a fishing vessel chartered by the Woods Hole Oceanographic Institution, was examined. For purposes of comparison, an excellent series of the Pacific species, *Apristurus brunneus* (Gilbert) was assembled from specimens collected from the research vessels of the University of Washington College of Fisheries and by the exploratory vessel *John N. Cobb* of the Bureau of Commercial Fisheries. Similarly a young example of *Cephaloscyllium uter* (Jordan and Gilbert) and also a series of the Pacific cat shark *Parmaturus xaniurus* (Gilbert) were obtained for comparison with Atlantic scyliorhinids from collections made by the research vessel *N. B. Scofield* of the California Department of Fish and Game. The type of *Scyllium laurussonii* Saemundsson was loaned by the Natural History Museum, Reykjavik, Iceland, for examination.

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No specimens from the coast of Argentina were seen. *Halaelurus bivius* (Smith) has been recorded from Argentina by Berg (1895), Lahille (1921, 1928), and Norman (1937). *Halaelurus chilensis* (Guichenot) mentioned by Lahille (1928) as a synonym of *Halaelurus bivius* (Smith) probably is a valid species and two species referrable to *Halaelurus* occur in Argentine waters according to information received from Professor Elvira M. Siccardi (personal communication). Professor Siccardi also found a population of *Scyliorhinus* on the coast of Argentina, either *S. boa* (Goode and Bean) or an undescribed species very similar to *S. boa*. Species found on the coast of Argentina are given very brief treatment here, based chiefly on photographs, measurements, and records of specimens that Professor Siccardi has kindly allowed me to see. Illustrations in this paper of *Halaelurus* are of specimens from Chile in the collection of the U.S. National Museum.

Ideal study series, that is, series including adults of both sexes, young in various states of growth, and specimens collected from a number of localities sufficient to outline the probable limits of geographical and vertical distribution, are not available for any of the 15 species treated here. For example: available specimens of *Scyliorhinus retifer* (Garman) satisfy ideal requirements except that no adult females with eggs have been examined; the series of *Apristurus riveri* Bigelow and Schroeder includes two adult males and three adult females, one with a partly extruded egg case, and a few young examples, material sufficient to show sexual dimorphism in the teeth of the adults and to show the oviparous habit, but the series lacks immature males.

Family SCYLIORHINIDAE

The definition of the family given by Bigelow and Schroeder (1948, pp. 195–196) is followed provisionally. Separation of the cat sharks from members of the family Orectolobidae on the basis of external form is comparatively simple when dealing with American material. No Atlantic American cat shark has barbels or has the nostrils connected with the mouth by a groove, while orectolobids in general have these characteristics. One Indian Ocean genus, *Conoporoderma*, referred to Scyliorhinidae by Bigelow and Schroeder, has barbels and another, *Haploblepharus*, does have the nostrils connected with the mouth by a groove. Otherwise the use of these characters to separate the Scyliorhinidae from the Orectolobidae is the most practical one. Of the characters given by Bigelow and Schroeder for separartion of the two families, Orectolobidae and Scyliorhinidae (1948, pp. 178 and 195), the only characterization of the Scyliorhinidae always applicable is that the scyliorhinids have three rostral cartilages, united at their tips; whereas orectolobids have none, one, or three rostral cartilages which are small and, if present, are not united at their tips. I have verified this only in a few western Atlantic species. Even tooth characters do not hold unless exceptions are noted. Adult males of *Apristurus riveri* Bigelow and Schroeder, instead of having small teeth with several cusps as in all other known scyliorhinids including female *A. riveri*, have single cusped teeth in about 20 median rows.

Grace White (1936), commenting on forms generally known as cat sharks, states that variation in the catuloids (cat sharks and allied groups) is so extreme as to make the distinction even among genera difficult. Certainly it is difficult to find family characteristics to which there are no exceptions and which set off scyliorhinids sharply from obviously related families. Although there has been reasonably general agreement on the kinds of sharks constituting the group known by the common name cat shark, precise morphological definitions of the family or families constituting the cat sharks and their allies have been various and apparently not entirely satisfactory even to those proposing the definitions. The cat sharks are, with few exceptions, small demersal forms of moderately deep water, and, again with exceptions, are not well known and are poorly represented in study collections. It is not unlikely that the group contains representatives of several evolutionary lines and that at the family level most of the classifications that have been proposed embrace horizontal groupings.

Müller and Henle (1841) placed all the sharks known by them to be egg layers in the family Scyllia, including both the scyliorhinids and the orectolobids without making a distinction between sharks in which egg cases are resorbed after formation or are retained in the oviducts until hatching (ovoviviparous species) and forms that discharge eggs in leathery cases at an early stage in

development (oviparous species). It has long been known that orectolobid species are either oviparous or ovoviviparous, but according to Bigelow and Schroeder (1948, p. 196), the scyliorhinids so far as known are oviparous. Poll (1951) and Cadenat (1959) subsequently reported the ovoviviparous condition in one species of *Galeus*. Probably more data will show that additional scyliorhinid species are ovoviviparous.

Regan (1908) separated the scyliorhinids and orectolobids as families and included *Pseudotriakis* in the Scyliorhinidae. He recognized only two other genera in the family and included especially divergent species within the genus *Scyliorhinus*. White (1937), with the intention of providing a vertical classification that would better reflect phylogenetic lines, proposed two new families, Aetelomycteridae and Halaeluridae, and retained the family Catulidae (= Scyliorhinidae). All genera of these three families of White excepting *Pristiurus* (= *Galeus*) were included in Regan's genus *Scyliorhinus*.

Bertin (1939) in a review of the classification of the cartilaginous fishes placed the cat sharks together with the orectolobids in the family Scyliorhinidae, but placed *Pseudotriakis* and *Pentanchus* in monotypic families. *Pseudotriakis* has a very long and low first dorsal fin with its base entirely in advance of the pelvic fins, and this is the primary morphological feature separating it from the scyliorhinids which have short-based dorsal fins (or single dorsal fin) located posteriorly, over or behind the pelvics. *Pseudotriakis* is represented by two large species, one, *Pseudotriakis microdon* Brito Capello, reported from the western Atlantic. Both species are larger than any known cat sharks. Although *Pseudotriakis* is not treated here as a member of the family *Scyliorhinidae*, its relegation to another family may not be warranted. The distinctive arrangement of tooth rows as diagonal bands characteristic of *Pseudotriakis* also occurs to a lesser degree in *Atelomycterus* and has some similarities to the tooth arrangement in *Apristurus*. Additional similarities are found between *Pseudotriakis* and the small scyliorhinid shark from the coast of Chile originally designated *Scyllium canescens* Günther, 1878.

Pentanchus profundicollis Smith and Radcliffe, 1912, was described from a single Philippine specimen as a notidanoid shark intermediate between the Hexanchidae and Chlamydoselachidae but with five gill openings instead of six or seven characterizing the former. It is so close to the scyliorhinids of the genus *Apristurus* in general appearance and details of gross structure, however, that except for the presence of only one instead of two dorsal fins, it would certainly fall within that genus. Regan (1908) was of the opinion that *Pentanchus* belonged in the family Scyliorhinidae and suspected that the absence of one dorsal fin was abnormal or accidental. Although additional specimens are not yet known, the type USNM 70260 is an adult male in fair condition. This specimen, disregarding the number of dorsal fins as a characteristic, does not fit the description of any known species of *Apristurus*. Furthermore, there is no evidence from external examination or the appearance in radiographs that the absence of a dorsal fin (absent from the position occupied by the first dorsal in *Apristurus*) is in any way a result of accident or structural abnormality. Short sections of the vertebral column from the trunk and caudal portions of the type were missing when I examined the type specimen but dissections had been carefully made somewhat off center and should not have affected fin-base vestiges had these been present. It appears to me that the separation of *Pentanchus* and *Apristurus* (as in Bigelow and Schroeder, 1948) is justified and that the two genera are properly to be placed in the family Scyliorhinidae.

Distribution and Segregation

About 58 species in 14 genera are known in the family Scyliorhinidae. With the exception of the Indian Ocean species, *Atelomycterus marmoratus* (Bennett), cat sharks appear very rarely in warm waters and inhabit shore waters only in the higher latitudes or in comparatively cool-water areas. The common rough-dog, *Scyliorhinus caniculus* (Linnaeus), of Europe, which figures as a laboratory animal in much of the physiological and experimental work on sharks, is an example of a species entering shallow waters. *Cephaloscyllium uter* (Jordan and Gilbert) of the California coast frequents relatively shallow water. In the western Atlantic one species is occasionally taken on the continental shelf north of the Carolinas and another species is said to frequent the shallow shore waters in the vicinity of Cape Horn, but from the

Carolinas to Argentina cat sharks are exclusively inhabitants of the continental slopes. Atlantic American records of *Apristurus* are for the most part from depths of 750 to 1500 meters, and lower latitude records of other cat sharks in the region are from depths of 200 to 750 m.

Along Atlantic American coasts, fewer hauls have been made in depths in excess of 1,000 m. than in shallower water and trawling has been limited in areas where rough bottom topography produced severe gear losses. Deficiencies in the representative quality of the collections are due chiefly to these factors.

Ford (1921), writing about *Scyliorhinus caniculus* at Plymouth, England, noted that there is a curious alternating seasonal predominance of the sexes in adults. In the winter the males were found to be the predominant sex, whereas in the summer the females were the more numerous. Differential preferences by the sexes for depth (and by inference for temperature) were noted by Springer (1960) in shallow-water carcharhinid sharks. This may be true also of some of the cat sharks. The importance of segregation by size as a means for protecting the young against predation by members of their own species is less apparent for cat sharks than for the large voracious carcharhinids, but perhaps is a useful trait. It is of interest in this connection that Ford (1921) reports *Scyliorhinus stellaris* feeding on the smaller *S. caniculus* in the Plymouth area.

Nearly all specimens of cat sharks from the western Atlantic have been taken in trawls. Most of those collected by exploratory vessels were caught in shrimp trawls having 1¾- or 2-inch mesh (stretched). Only the smallest sizes, less than 6 inches, would be able to escape through the meshes; larger cat sharks, over 24 inches long, might sometimes evade the nets.

WESTERN ATLANTIC GENERA

The cat sharks known from the western Atlantic fall into five well marked groups corresponding to the five genera recognized here. Differences of species within genera in the western Atlantic are not great except between the two species of *Halaelurus* reported from Argentina. Of the five western Atlantic genera, one genus, *Apristurus*, is probably cosmopolitan in waters of suitable depth outside of Arctic and Antarctic Regions. *Galeus* is present both in the North Atlantic and North Pacific Oceans but has not yet been found in the Southern Hemisphere if recognition is accorded Whitley's genus *Figaro* (1934). *Schroederichthys* is restricted to the Caribbean and tropical Atlantic. Western Atlantic members of the genus *Scyliorhinus* form a compact infrageneric group differing less from one another than from species found in the eastern Atlantic or in the western Pacific. *Halaelurus*, as understood here, includes species from the Indo-Pacific region and the Southern Hemisphere.

The area of marine situations suitable to most of the species of cat sharks is very small in comparison to the total ocean area. *Apristurus*, which on Atlantic American coasts is found most commonly at depths from 750 to 1,500 m. and may range into deeper water, occurs over a much greater geographical area than species of other genera, possibly being present in ocean basins of moderate depths. Figure 1 showing the extent and distribution of bottom along the Atlantic coast of temperate North America at depths between 100 and 500 fathoms illustrates the rather narrow bands in some areas to which cat sharks may be restricted. Along tropical and subtropical western Atlantic continental slopes, the ranges of cat sharks other than *Apristurus* are extremely narrow bands.

The largest of the western Atlantic species probably do not ordinarily attain a length as great as 80 cm., and the smaller species (one species of *Scyliorhinus*, one *Apristurus*, the three American *Galeus*, and *Schroederichthys*) probably do not exceed 50 cm. Some eastern Atlantic and South African species are larger. *Scyliorhinus stellaris* (*Linnaeus*) of the eastern Atlantic reaches a length of 150 cm. in the Atlantic but only about 75 cm. in the Mediterranean (Tortonese, 1956). Smith (1949) gives maximum sizes of 4 feet (122 cm.) or more for *Scyliorhinus capensis* (Müller and Henle) and *Conoporoderma africanum* (Gmelin) of South African coasts.

At the present time, a revision of the family involving a review of generic or family classifications using some of the more advanced modern methods that are available is impractical because insufficient descriptive data exists for most named species. Furthermore, it is very likely that a rela-

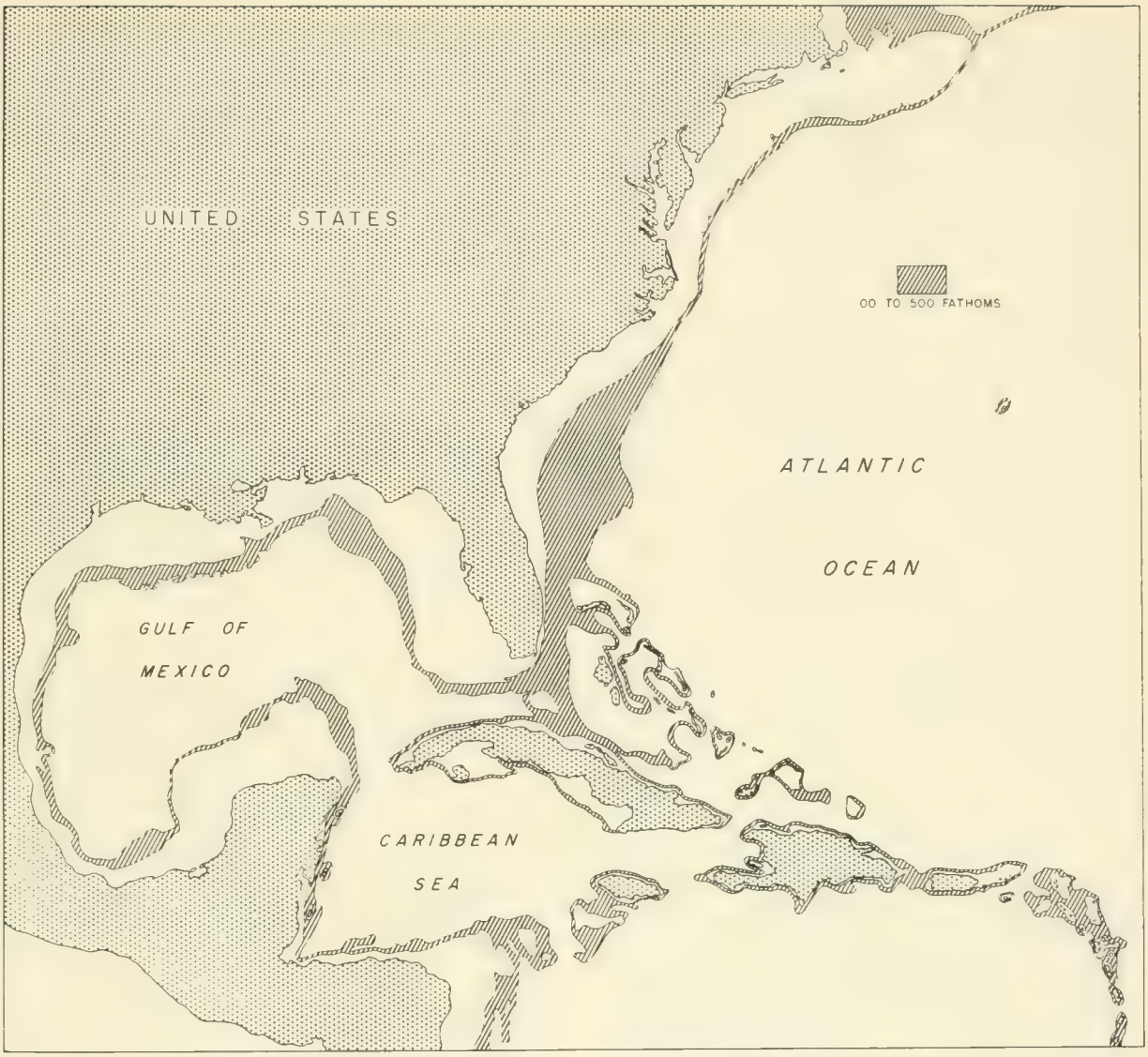


FIGURE 1.—More than 95 percent of the specimens of scyliorhinids from the western North Atlantic available for study have been collected within the 100- to 500-fathom (183- to 914-m.) depth range shown here.

tively large number of unnamed species exist, undescribed not because their differences from other species have not been recognized, but undescribed because examples have not yet been caught. For this study, more than half the specimens have been collected within the past five years.

To anticipate in detail the needs of future studies is presumptuous, but some of the characters of the genera of the cat sharks of the western Atlantic that have been little used in orthodox or classical studies seem worth discussion even though these cannot be fully utilized in reaching taxonomic decisions in this geographically limited study.

Color and color pattern

Western Atlantic cat sharks fall in two groups with respect to color pattern. All *Apristurus* are nearly uniform in color, and preserved specimens are either black or dark brown of various shades but with no tendency to the formation of any pattern. A few specimens that I have seen brought to the surface from hauls in the northern Gulf of Mexico were uniform black, but these became either very dark gray or dark brown after

preservation. Areas of skin not covered by denticles, around the gills for example, remained darker; and edges of fins, where denticles are sometimes either more numerous or are absent, became a different shade of brown or black than the rest of the body surfaces after preservation. The material examined suggests that there is no diagnostic significance to brown or black color in museum specimens because color changes variously after preservation.

Excepting *Apristurus*, all Atlantic American cat sharks now known are somewhat darker above and lighter below, and furthermore, all have some pattern of spots, blotches, or lines on the dorsal surfaces, either lighter or darker than the background color. This does not pertain outside the western Atlantic where the genus *Galeus*, for example, is represented by some species without markings, at least as adults, and other genera, *Parmaturus* for example, are represented by species that are uniformly dark.

The two species of western Atlantic *Galeus* have color patterns that differ in intensity among the three forms but show more resemblances to one another than to color patterns in any other genus. The patterns in *Galeus* are complex and difficult to describe. Because pattern differences in this genus are obscured by differences in intensity of pattern, they are of low value in field identification and other characters are not only more easily described but also may be more reliable.

Species of the three other genera as represented in the western Atlantic, *Scyliorhinus*, *Schroederichthys*, and *Halaelurus*, have essentially similar basic color patterns but have diagnostically useful modifications of the basic patterns. As indicated by the few species of which juvenile examples are available, and in its simplest and most persistent form, the basic pattern consists of a series of seven dorsal saddles or blotches. Depending upon species, either more saddles may be present in intermediate positions or some of the main saddles may be obscure.

A parallel development of pattern in *Scyliorhinus torrei* Howell-Rivero and *Schroederichthys maculatus* (one of the new species described here) illustrates this. Both species have the seven dorsal saddles appearing in some individuals but generally more prominent in the young. In adults of both species, however, the saddles may become quite indistinct with a partial substitution of a pattern of small white spots on a tan background color. The tan color here is the color in life and is not brought about by preservation. The saddles seem to become more distinct with preservation. In life or when freshly preserved the two species are so similar in appearance of the color and pattern that the rather great structural differences may be overlooked easily.

Variation in pattern within species in the material at hand is moderate and reasonably well defined. Figure 2A shows a rather extreme example of the absence of full development of a reticulate pattern characteristic of *Scyliorhinus retifer* (Garman), whereas figure 2B shows a specimen with the reticulate pattern fully, but not uniformly, developed. Although this pattern is variable, it can be distinguished readily from patterns made up of discrete black spots or white spots.

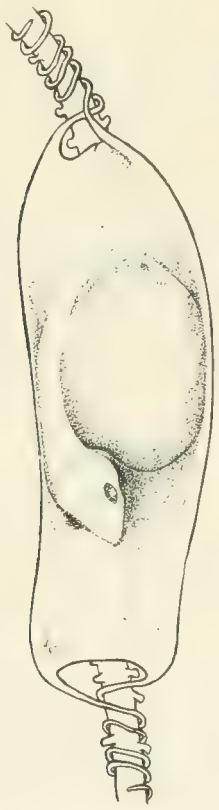
Reproduction

Most cat sharks lay eggs in cases which, when first laid, are impervious and sealed against the entry of seawater. During development of the embryo, slits appear in corners of the egg cases to permit a flow of sea water through the egg case. Tendrils, one from each of the four corners of the egg case, attach it to objects on the bottom when the eggs are laid.

In addition to information on the egg laying habits of *Apristurus riveri*, available records and material show that *Scyliorhinus retifer* and *Schroederichthys maculatus* lay eggs. No positive information is at hand for other western Atlantic species, but an egg case with developing embryo (fig. 3) may be presumed to be either *Scyliorhinus meadi* or *S. torrei* on indirect evidence of locality.

The genus *Galeus* is represented in the eastern Atlantic, including Icelandic waters, by four species among which are two little-known forms without markings or color patterns; these were described from specimens from the Hebrides and from Iceland. The remaining eastern Atlantic forms include *Galeus melastomus* Rafinesque, an egg layer, and *Galeus polli* Cadenat, an ovoviviparous species that retains eggs in the oviduct until after the egg shell has been absorbed and after the embryo has completed absorption of the yolk sac. No positive evidence has been found to

FIGURE 2.—*Scyliorhinus retifer* (Garman): A, Drawn from a 465-mm. female; B, drawn from a 380-mm. female. Both specimens collected in 365–385 m. off Pensacola, Fla. The upper figure shows a specimen with seven major saddles but with the addition of one intermediate saddle between the two dorsal fins. The darker reticulations in the lower figure can be seen to delineate seven major saddles.



show whether or not western Atlantic species produce living young. Probably both western Atlantic species are ovoviviparous. No shelled eggs have been found in oviducts of the many adult female specimens that have been examined, and no unidentified egg cases small enough to belong to *Galeus* have been seen.

Claspers and clasper siphons

Leigh-Sharpe has proposed that more consideration be given to the structure of the claspers and clasper siphons or clasper glands in taxonomic studies of elasmobranchs. In a series of papers published between 1920 and 1926 he described these

FIGURE 3.—Egg case of a cat shark collected off Cape Kennedy, Fla., showing a developing embryo within its entirely transparent and colorless case and showing the characteristic method of attachment of the case. The degree of transparency of the egg case, the shape, and the nature of surface markings on it vary with species. Transparent egg cases which may be quite free from color when fresh may become brownish after storage in alcohol. The embryo color pattern and the site of collection of the egg case suggests that it is *Scyliorhinus meadi*. Drawn from an egg case approximately 1.4 by 4.0 cm. exclusive of tendrils.

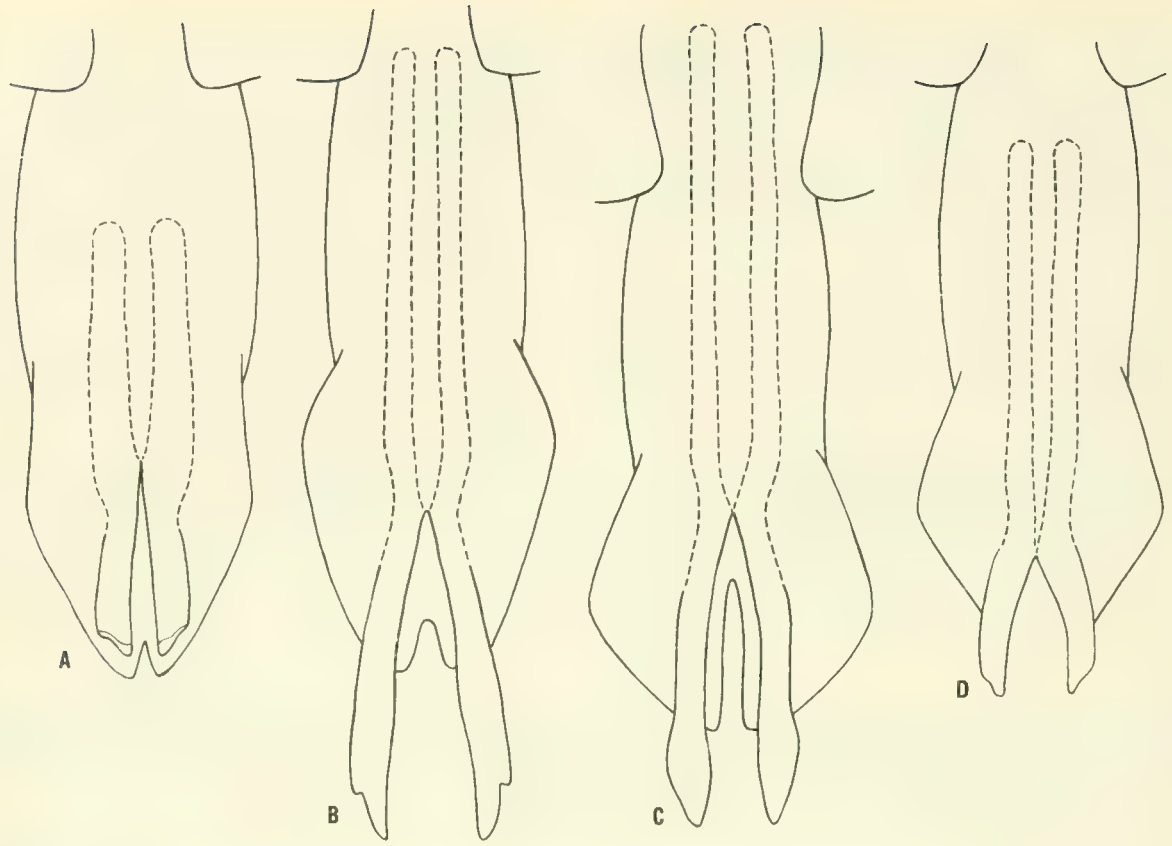


FIGURE 4.—Diagrams showing general shapes of claspers and clasper siphons in adult male cat sharks: A, *Scyliorhinus torrei* and B, *Galeus arae*, both from the Florida Straits; C, *Schroederichthys maculatus* from the western Caribbean; and D, *Apristurus riveri* from the southwestern Caribbean. Each drawn to scale but scales are unequal.

structures in some scyliorhinids in detail (Leigh-Sharpe 1920, 1922, 1924, 1926a, and 1926b). In practical application for taxonomic studies, however, there is some difficulty because of inadequate series of specimens. Of the 15 western Atlantic scyliorhinids treated here, for example, adult male specimens were not available for 6 species.

Diagrams outlining the general size and shape of claspers in relation to the pelvic fins and outlining roughly the extent of the clasper siphons are shown in figure 4 for representatives of four western Atlantic genera. No important differences in gross examination were noted among adult males of the two species of western Atlantic *Galeus*. Supplementary examination of a few adult male *Galeus* from the eastern Atlantic and from the Pacific failed to reveal substantial differences in clasper structures within the genus excepting the presence of hooks on specimens of western Atlantic species examined and the absence of these on the only eastern Atlantic adult male available. The available material is insufficient to show whether clasper structures of western Atlantic scyliorhinids are useful in the diagnosis of species, but from a necessarily cursory review it appears that they might be quite useful as generic characters.

Hooks were present on claspers of the species of *Galeus* but were absent on *Apristurus* and *Schroederichthys* and from the claspers of western Atlantic *Scyliorhinus* examined. Hooks were not found on a clasper of one *Galeus melastomus* from the eastern Atlantic.

The denticles on the surfaces of claspers in all of the specimens examined have their points directed forward toward the base of the clasper. The reversal of direction of the denticles is noted as occurring in *Scyliorhinus stellaris* (=*Scyllium*

catulus) by Leigh-Sharpe (1920) and apparently is a feature common to all galeoid sharks but not to sharks of other suborders.

Shape of body and fins

The caudal axis in the family Scyliorhinidae is little elevated and, excepting adults of *Scyliorhinus*, the overall shape of western Atlantic species is slender. One genus, *Schroederichthys*, has a very elongate postpelvic trunk region.

The length of the body cavity relative to the overall size of the fish (volume) differs considerably in the four genera found in the tropical and northern Atlantic. This difference is reflected in the size of the liver and it appears likely that with sufficient material for study it would be found that liver characteristics would be useful as taxonomic criteria. The general shape of the liver is shown in figure 5.

A series of Pacific *Apristurus brunneus* examined in comparison with *Apristurus riveri* from the Atlantic show some apparently constant differences in liver shape. In *A. brunneus* the liver is larger and in most specimens the right and left posterior lobes are united for most of their length, excepting only that part just anterior to and extending past the cloaca. In *A. brunneus* the liver almost completely covers the visceral cavity when viewed from the ventral aspect. Only the falciform ligament and the rectum are visible in addition to the liver when the body cavity is opened ventrally. Thus it would seem from casual inspection that large ripe eggs from the ovary located under the liver when viewed from the ventral aspect (only right ovary functional in scyliorhinids) would have to make a remarkably long or tortuous journey to reach the opening of the oviducts.

It may be significant in indicating possible derivation of the orectolobids which have quite short snouts with reduced or absent rostral cartilages, that western Atlantic *Scyliorhinus* and *Halaelurus* have relatively short snouts, *Schroederichthys* has a moderately short snout, but both *Galeus* and *Apristurus* are long-snouted. Associated with the long snouts of *Galeus* and *Apristurus* is the comparatively greater prominence of the external pores for the Ampullae of Lorenzini. The extensive pore system of the Ampullae of Lorenzini in *Apristurus* may be associated with its habitat

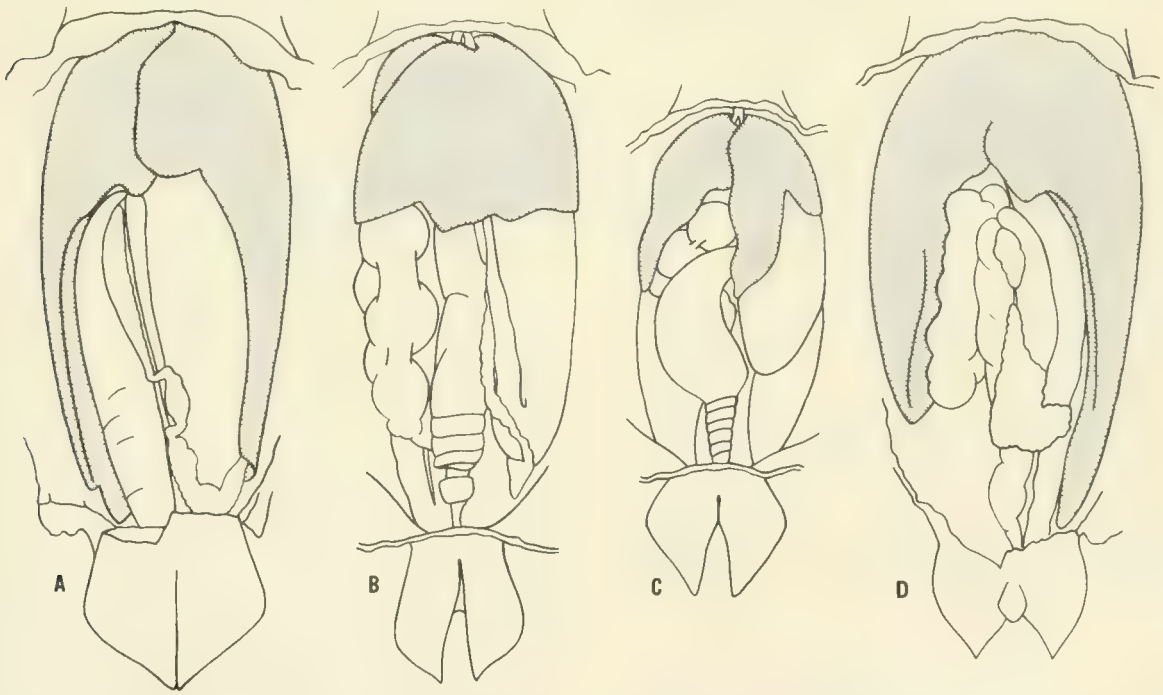


FIGURE 5.—Diagrams of the arrangement of visceral organs showing liver shapes (stippled areas) in representatives of four western Atlantic genera: A, *Scyliorhinus retifer;* B, *Galeus arae;* C, *Schroederichthys maculatus;* and D, *Apristurus riveri.*

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which is in comparatively deeper water than any of the other cat sharks. Pineal windows were not seen in the specimens of *Apristurus* or any other cat sharks examined. Among sharks, these are consistently present in the squaloid genus *Etmopterus*, members of which are black.

Dermal denticles

The size, arrangement, and structure of dermal denticles are often quite useful characters for practical problems in identification of sharks. Ordinarily the typical dermal denticles used in descriptive accounts of species are those from a lateral surface near the first dorsal fin but below the middorsal line. Here, unless some specific location is indicated, denticle descriptions are from denticles taken at a point about halfway along a line between the axil of the pectoral fin and the origin of the first dorsal fin. In some instances, differences in the denticle structure are the most reliable and definite means of determining species. For example, *Squalus blainvillei* is readily distinguished from *Squalus cubensis* by great differences in denticle shapes. Among scyliorhinids of the western Atlantic, denticle differences are either less well marked or need qualification as to location or as to the size or age of the specimens involved in comparisons.

In *Scyliorhinus retifer* the denticles increase in size as the shark becomes larger and the denticles change somewhat in shape. In some sharks it is evident that the number of denticles increases as the shark grows large, but in the series of *S. retifer* examined, positive evidence of an increase in the number of denticles with increasing size was not apparent in a cursory examination. The general aspect of a section of skin surface with denticles is shown in figure 6.

In *Scyliorhinus retifer* denticle shapes on different parts of the body vary and the variation follows a pattern more or less characteristic of all galeoid sharks. On the ventral surfaces the denticles have much less prominent ridges and the lateral points are generally absent. On leading edges of fins the denticles are usually smoother and flattened so that there are no projecting points. On the head and especially those parts of the head used sometimes for bumping objects, the denticles are somewhat shorter with thicker edges or points.

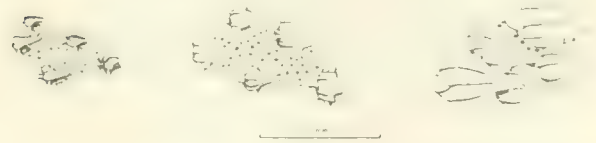

FIGURE 6.—Dermal denticles from a series of female *Scyliorhinus retifer* from the Gulf of Mexico. Left from a specimen 175 mm., center from a 295-mm. specimen, and right from a 465-mm. specimen. Camera lucida drawings to the scale indicated.

Denticles of *Galeus* and *Apristurus* follow this plan to a less marked degree. The denticles of ventral surfaces are about the same shape as those of the dorsal surfaces, but their construction is lighter.

Specialized dermal denticles forming a crest along the upper margin of the caudal fin are found on all species of the genus *Galeus*, varying slightly among species but probably not sufficiently to be used in practical field identification. The genus *Figaro* Whitley has been described from Australian waters and differs in having the specialized scales on both the upper and lower margins of the caudal fin. The eastern Pacific genus *Parmaturus*, quite unlike *Galeus* in many respects, has a denticle crest on the upper caudal fin margin.

Although not having a definite crest, *Apristurus profundorum* has several rows of compactly arranged, imbricate denticles along the upper margin of the caudal fin. The body and sides of the fins in that species are quite sparsely clothed with denticles which are nearly erect.

The young of *Scyliorhinus caniculus* and *S. stellaris* have a series of enlarged scales, one series on each side of the middorsal line extending from the shoulder area back to the first dorsal fin. According to Ford (1921), these scales are visible in embryos of *S. caniculus* taken at Plymouth, England, when the embryos are 44 mm. long. They persist for a short time after hatching, but similar scales are present on *S. stellaris* and may still remain in place until the sharks are over a foot long.

Enlarged scales are present on an embryo (fig. 8) presumed to be *S. retifer*. They are not visible in specimens of 150 mm. or more, but on specimens of newly hatched *S. retifer* they are represented sometimes by a series of scars. Enlarged denticles in a similar position but widely spaced are present in *Halaelurus* from Chile, usually surrounded by a ring of somewhat modified smaller denticles. Series of enlarged denticles are present on both

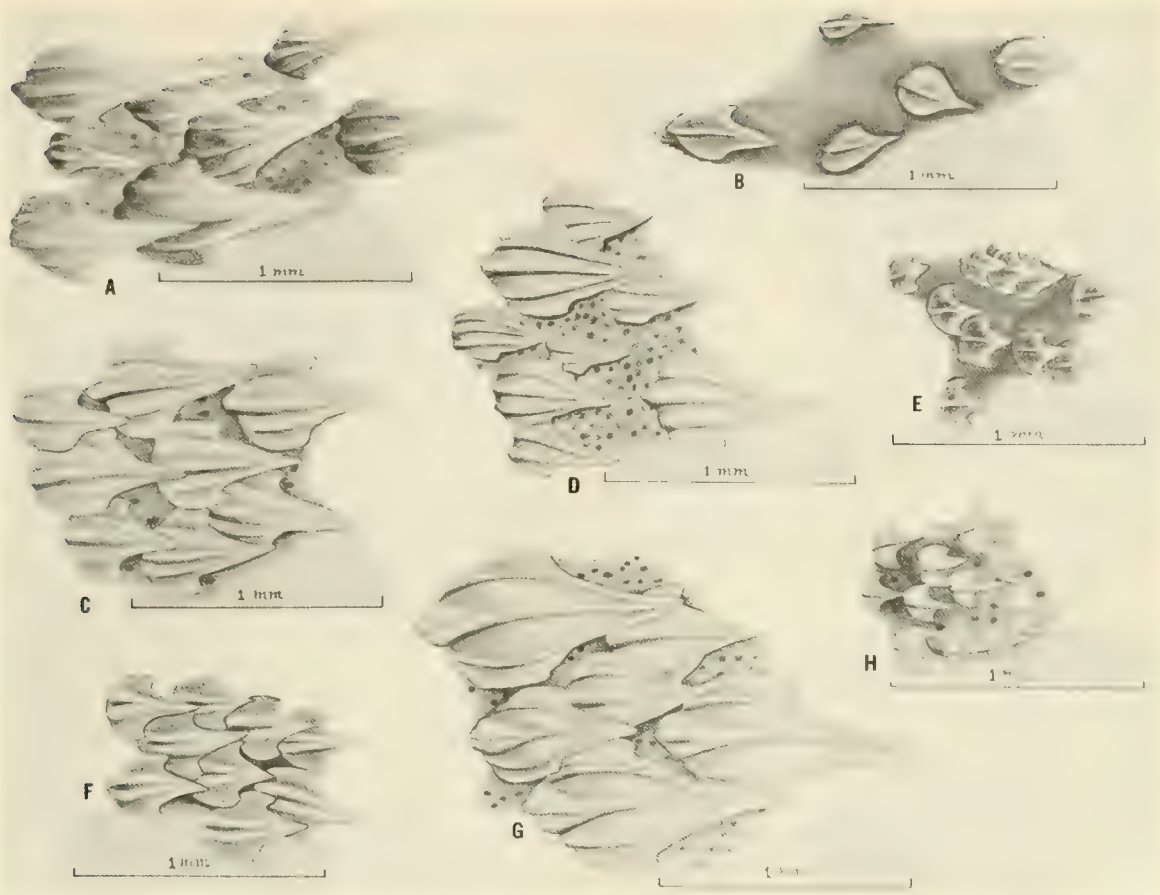

FIGURE 7.—Camera lucida drawings of denticles from some western Atlantic catsharks: A, *Scyliorhinus meadi* from 264-mm. immature male; B, *Apristurus profundorum* from 380-mm. immature female; C, *Scyliorhinus torrei* from 243-mm. adult male; D, *Scyliorhinus hesperius* from 296-mm. immature male; E, *Apristurus riveri* from 450-mm. adult female; F, *Schroederichthys maculatus* n. sp., from 295-mm. adult female; G, *Scyliorhinus retifer* from 410-mm. adult male; H, *Galeus arae* from 287-mm. immature female. Note: Denticles of *Apristurus profundorum* are more erect over most of the body surfaces than shown here, their points projecting almost perpendicularly from the plane of the skin surface.

sides of the middorsal line of a 160-mm. specimen of *Cephaloscyllium uter* from Monterey Bay, Calif.

Teeth

The teeth of scyliorhinid sharks are small, most commonly with a larger central cusp having one or more smaller lateral cusps on each side. In some species of *Apristurus* the teeth nearer the corners of the mouth may have many cusps (as many as nine have been noted) with the central cusp but little higher than adjacent ones. In *Atelomycterus* from the Indo-Pacific, the cusps of some of the teeth near the corners of the mouth are much reduced and the rows are fitted so close together as to form an almost smooth grinding surface.

Except for specimens of *Apristurus*, the tooth form does not vary greatly in the scyliorhinid specimens examined from the western Atlantic and it is probably impractical to attempt to distinguish most species from teeth alone. Western Atlantic *Apristurus*, as a general rule, have teeth with more cusps and, in some *Apristurus*, crowding of some of the lateral cusps in front of the central cusp (see fig. 9D) is frequent.

In *Apristurus riveri* the most extreme tooth dimorphism yet reported for sharks occurs. The two adult males that constitute our entire series of

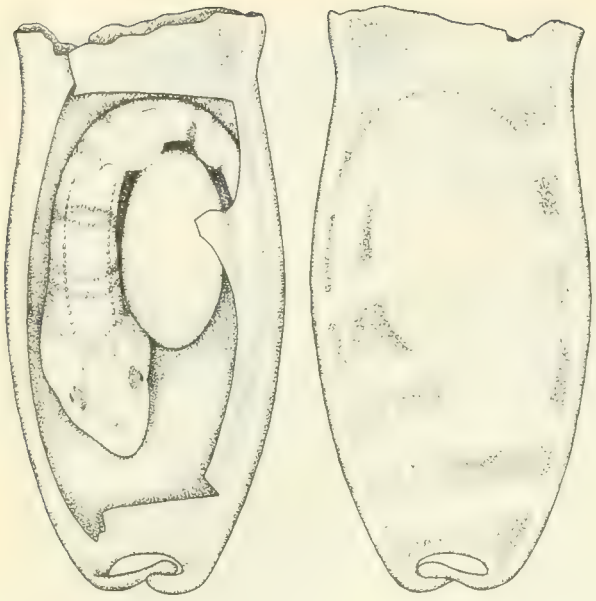

FIGURE 8.—Egg case of a cat shark collected from 100 fathoms off the coast of North Carolina, showing an embryo with the two series of enlarged denticles that characterize the young in some species of scyliorhinid sharks. Presumably this is an embryo of *Scyliorhinus retifer*. The somewhat opaque white banding in the shell has not been reported previously and may not always be evident in egg cases of the species.

males of that species not only have teeth twice as long as the teeth of females of comparable size but the teeth of the males are also quite different in shape from those of the females, with lateral cusps entirely absent on the teeth of the central part of the jaws. A few teeth with lateral denticles or cusps are present among the last few rows toward the angles of the jaws.

This degree of dimorphism illustrated by the accompanying diagram (fig. 10) does not occur in the other species of *Apristurus* that are represented by sufficient material to check. The teeth of males of the Pacific species, *Apristurus brunneus*, are somewhat larger than the teeth of females of comparable size, but there is no important difference in tooth shape. No significant dimorphism is present in A. *profundorum*, A. *indicus*, *or* A. *laurussoni*.

It is suggested that the modification in teeth would function effectively to hold the female, perhaps by the pectoral fin, during copulation.

With reference to *Halaelurus* from Patagonia, Vaillant (1891) states that one finds great vari-

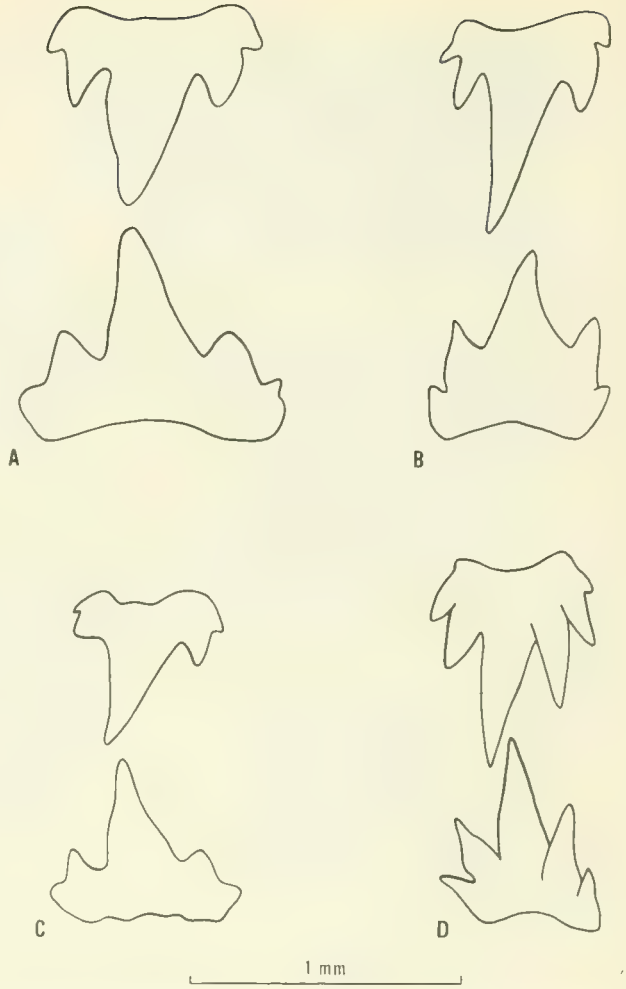

FIGURE 9.—Camera lucida outlines of teeth from upper and lower jaws, shark's right side, fifth lateral row counting from the symphysis: A, *Scyliorhinus hesperius*, a 272-mm. female; B, *Galeus arae*, a 365-mm. male; C, *Schroederichthys maculatus*, a 220-mm. male; and D, *Apristurus indicus*, a 430-mm. female.

ation in the teeth of the lower jaw with differences following size and perhaps sex. Also in a table of differences between *Scyllium bivium* and *S. chilense* (*Scyllium*=*Halaelurus*), Vaillant notes that the lower jaw teeth of *bivium* are not very small and are either without lateral cusps or with lateral cusps not very distinct, whereas the teeth of the lower jaw in *chilense* are very small and have no lateral points. In spite of complications of nomenclature and contradictions in the literature, it is obvious that South American *Halaelurus* exhibit a transition in tooth form. A more thorough study is necessary to determine whether

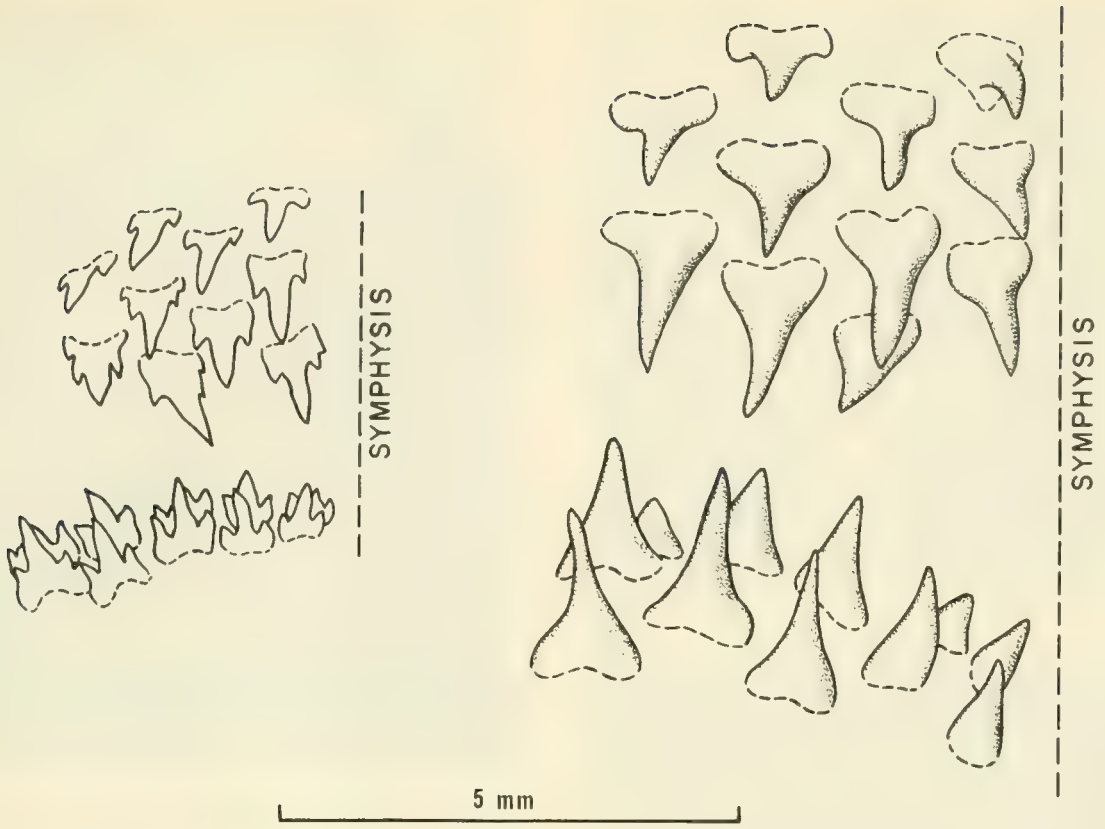

FIGURE 10.—Camera lucida outlines of teeth of 405-mm. adult female *Apristurus riveri* (left) compared with same scale outlines of teeth of 430-mm. adult male (right) both specimens from 860- to 914-m. depth off the Caribbean coast of Panama.

changes in tooth form occur at sexual maturity or whether several species with different tooth forms are involved with or without changes during growth. South American *Halaelurus* (not including the deeper water form *Scyllium canescens* Günther) shows a trend toward development of spike dentition in the lower jaw. Spike teeth in the lower jaw and cutting teeth in the upper jaw always characterize species of the larger and more specialized galeoids wherever differences in apparent function between upper and lower jaws exist. In contrast, in the notidanoids and squaloids it is the upper jaw that has spike teeth.

It has been customary to express a tooth formula for extant sharks simply as the number of teeth in the upper jaw over the number of teeth in the lower jaw. In sharks having only one functional band of teeth, the counts are rather easily determined. In *Carcharhinus leucas*, for example, this would be 27/25 where 27 is the number of teeth on the upper jaw and 25 is the number on the lower jaw. A refinement of this kind of formula, used for example by Bigelow and Schroeder (1948), breaks down the count to indicate the number of very small teeth at or near the jaw symphyses. In *C. leucas* such a count might be expressed as 13+1+13/12+1+12, where 13 is the number of teeth on each side of the upper jaw, 12 the number on each side of the lower jaw and 1 represents the number of very small teeth at the symphysis. Leriche (1905) developed a classification of the various types of teeth found in the jaws of fossil sharks which permits the use of a more descriptive and meaningful formula to express conditions found in various species. Applegate (1965) has proposed some modification of the Leriche system and an extension of its use to extant species. This system has obvious merits although its formulas are perhaps less informative about scyliorhinids than about species in most

other shark families. No attempt has been made to use it here because of this and because only about half the scyliorhinid genera are being reviewed.

Strasburg (1963), in discussing tooth replacement in a squaloid species, *Isistius*, used the terms independent dentition, alternate overlap, imbricate overlap, and mixed alternate and imbricate overlap to describe the arrangement of teeth in a transverse band and to distinguish these arrangements from the modified imbricate overlap found in *Isistius*. He found no pure alternate dentition in the species he examined, but these did not include a scyliorhinid.

In scyliorhinids several transverse series of teeth are functional. For the purposes of this discussion a series of teeth is defined as a file or array of teeth along a single line running parallel to the jaw cartilage axis from one corner of the jaw opening to the other. A row of teeth on the other hand is defined as a file of teeth in a line extending from a germinal area on the inner surface of the jaw to the outer rim of the jaw or lip. Rows of teeth are frequently, but not always, arranged in a line on a plane perpendicular to the axis of the jaw cartilage.

In all scyliorhinid sharks several series of teeth are functional, and in addition two or more series of developing teeth are present along the inner side of the jaw. The developing teeth are covered there by the lining of the mouth which forms a protected space in which tooth buds form. In *Scyliorhinus*, *Galeus*, and *Schroederichthys* four or five functional series are usually present in each jaw and in *Apristurus* five or six functional series. Impressions or scars of tooth bases are often visible at the outer ends of tooth rows. If two series are considered together as one band, the arrangement is alternate, the teeth in the outer series being present in half the tooth rows with their bases overlapping the alternately occurring teeth of the next functional series. The teeth of all specimens of scyliorhinids examined were somewhat crowded with a considerable degree of overlap (see fig. 11). Alternate dentition with less crowding is to be found in some sharks of other groups. The arrangement of teeth which, following Strasburg (1963), would probably be called modified alternate dentition if found in *Pristiophorus*, but with less crowding has a quite different appearance from the typical arrangements in scyliorhinids. In *Pristiophorus* (fig. 12) the number of rows of teeth are readily counted, and no confusion results from the appearance of diagonal files of teeth.

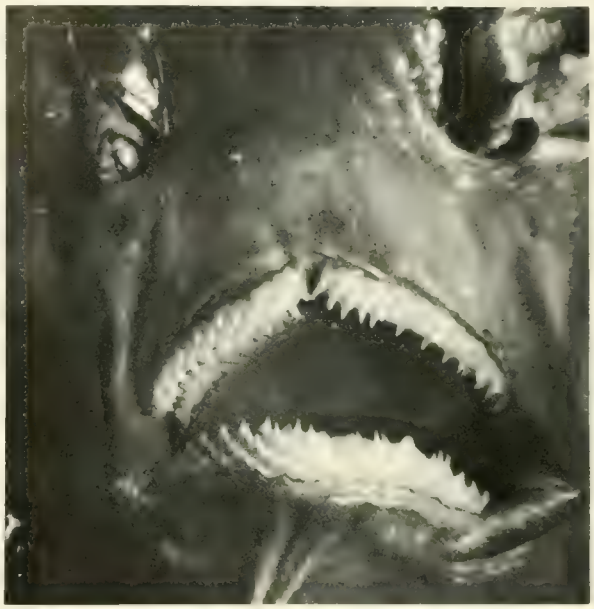

FIGURE 11.—Head of a 430-mm. adult male *Apristurus riveri* showing diagonal files of teeth in the lower jaw at the left side of the photograph. Dentition in this specimen is alternate throughout. Reflections from base of some of the teeth appear in the photograph to depict accessory cusps, but in reality none are present on teeth that are shown in the photograph.

The presence or absence of a separation of the teeth of one side of a jaw from teeth of the other side by a band of fleshy material seems to be a variable in the scyliorhinid specimens examined. Many specimens of *Apristurus* have such a separation either in the upper or lower jaw or both, whereas some do not. Furthermore this variation occurs in series of the same species. The extent to which this variation may be the result of stretching of ligaments at the symphysis has not been determined.

The number of tooth rows in some scyliorhinids is difficult to count for a variety of reasons. The teeth are small, and toward the angles of the jaws low-crowned multicusped teeth are not clearly defined. The teeth are crowded, and in a few specimens, or perhaps a few species, the arrangement of the teeth is not a simple alternate arrangement but is mixed. Similarities between the cat sharks,

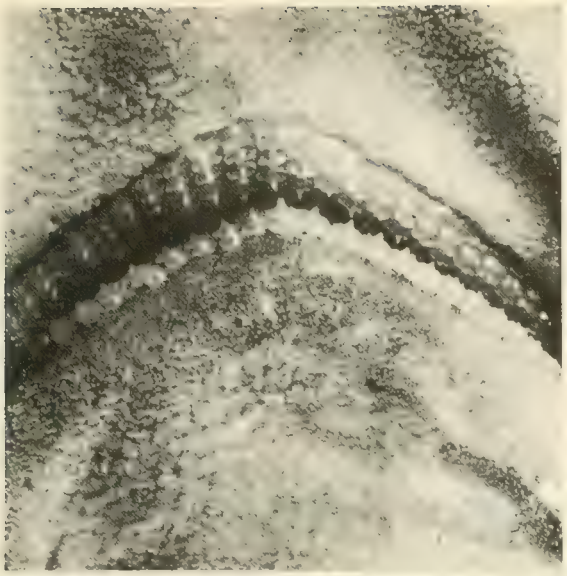

FIGURE 12.—Teeth of the saw shark, *Pristiophorus schroederi* (Pristiophoroidea), showing a modified alternate tooth arrangement differing from the arrangement found in the *Scyliorhinidae* (Galeoidea) chiefly in the lesser degree of crowding. Photograph by Los Angeles County Museum.

Scyliorhinidae, and the false cat sharks, Pseudotriakidae, already have been noted. The upper and lower jaw teeth of *Pseudotriakis microdon* Bocage and Capello are illustrated in Bigelow and Schroeder (1948) and are described and discussed in more detail by Jaquet (1905). The arrangement of teeth in the lower jaw in *Pseudotriakis* and *Apristurus* have some similarity in appearance due to the rather well defined diagonal files of teeth. Gross examination of the type specimen of *Pseudotriakis acrages* Jordan and Snyder (SU 12903) shows the diagonal files of lower jaw teeth continuing widely separated, but with the teeth within a file quite close together, back to the germinal area (see fig. 13). This appears to indicate a diagonal movement of the teeth from the area of budding into the functional position, but such an explanation is superficial. A study of the comparative histology of the developing teeth in several families of sharks should prove helpful in indicating relationships.

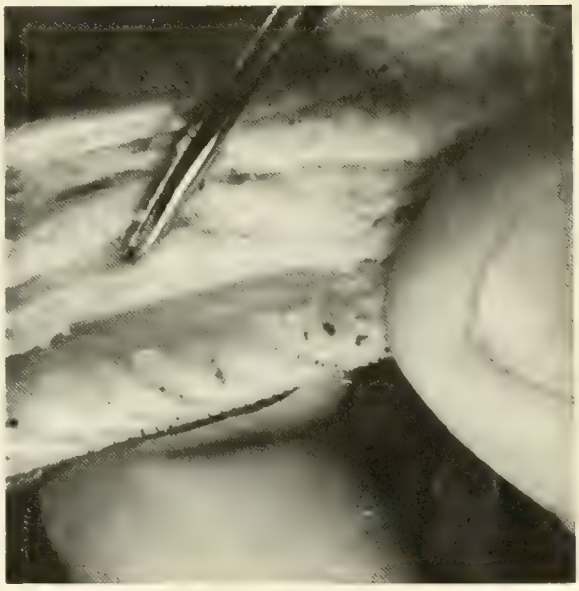

FIGURE 13.—Upper photograph showing diagonal files of teeth in the lower jaw of the type specimen of *Pseudotriakis acrages* Jordan and Snyder (SU 12903). Lower photograph, same jaw rolled outward with the tooth germinal area exposed and showing continuation of the files diagonally on the dental lamina where they become progressively smaller and softer to the point of their apparent origin.

NUMBER OF VERTEBRAE

Vertebrae were counted from radiographs of specimens of the family, but the diplospondylous vertebrae near the tail tips were difficult to count. Furthermore, in some radiographs it was not possible to determine whether all of the terminal vertebrae appeared. Since it was always possible to

count the number of monospondylous vertebrae with confidence, only these counts are given here (table 1).

The series reported here is too small for definitive use, but is sufficient to give promise that a more comprehensive study would be helpful in species diagnosis. Several kinds of interpretive factors may require consideration in a more comprehensive study. Some variation in meristic characters would not be surprising in a sample collected over a large geographical range. In our series of 33 counts from *Apristurus indicus*, the counts vary from 35 to 41, and localities of capture range over 20 degrees in latitude. In the series of 25 counts for *Apristurus laurussoni* a single count, higher than the cluster, is the count for the holotype, taken about 20 degrees north of any of the other specimens of the series.

The reliability of counts of vertebrae for purposes of numerical analysis or for identification is reduced because of abnormalities occasionally present. In the distribution of counts in 34 specimens of *Schroederichthys maculatus*, for example, where 33 are clustered but one count is somewhat apart, the high count in this specimen appears to be attributable to an uneven transition to diplospondyly. Here a few displospondylous vertebrae appeared well forward in the trunk region.

MORPHOMETRICS

The conventional ways to measure sharks are comprehensively illustrated by Garrick and Schultz (1963, figs. 1A and 1B), and this system of measurement is used here insofar as possible. Unfortunately measurements very useful for some sharks are difficult to apply to others. In the scyliorhinids, for example, the axis of the caudal fin is not perceptibly elevated and the point at which the upper lobe of the caudal fin begins is merely an estimate. The fins of scyliorhinid sharks, especially *Apristurus*, are soft and are generally rounded or lobelike structures making fin measurements difficult to define.

Most diagnostic accounts of scyliorhinids rely greatly upon morphometrics as key characters to separate species or genera. These characters are at least accessible and their use does not require a microscope. As applied to scyliorhinids, however, some kinds of comparative measurements seem to be particularly unreliable.

In comparing fin sizes, for example, the statement that the length of the base of the anal is 4 times the length of the base of the first dorsal fin in one species, but only 2½ times the length in another species, introduces a variety of difficulties in practical application. Precise measurements of the length of fin bases are not easily made because of the gradual slope of the forward end of the fin. This is sometimes complicated by the distortion or shriveling of the specimen in preservation. The lengths of fin bases may vary independently. Thus a comparison that seems quite clearly to differentiate species when some specimens are compared may be quite inadequate for other specimens.

In scyliorhinids there are occasionally specimens having much longer gill slits on one side than on the other, and gill slits are especially subject to distortion in length or even in position by preservation.

The ease with which data on measurement can be communicated and the difficulty of correctly and adequately describing shape seem to have led to overemphasis of measurements and less than

TABLE 1.—*Frequency of occurrence of various numbers of monospondylous vertebrae in some western Atlantic cat sharks*

Species	Number of monospondylous vertebrae																			
	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49
Scyliorhinus retifer											2	5	8	7	1						
Scyliorhinus boa												4		1		1					
Scyliorhinus meadi															1			1		2	1
Scyliorhinus hesperius											2	3	2	1							
Scyliorhinus torrei		1	3	2	3	2															
Schroederichthys maculatus	6	22	3	2			1														
Schroederichthys tenuis				1		1															
Galeus arae					1	12	14	8	2												
Galeus cadenati					4	7	1	1													
Apristurus profundorum					1	1	4	1													
Apristurus riveri		1	6	3																	
Apristurus indicus							2	1	4	13	8	4	1								
Apristurus laurussoni									3	2	8	7	4		1						

desirable treatment of other characters. Measurements remain useful in description, but some better balance and the use of a large number of characters, including some that can best be described in illustrations, seems desirable and perhaps necessary for a revision of the family.

KEY TO GENERA OF WESTERN ATLANTIC SCYLIORHINIDAE

The following key to western Atlantic genera is sufficient for their separation, but the degree of difference between them is better illustrated in the chart given as table 2.

KEY TO WESTERN ATLANTIC GENERA OF SCYLIORHINIDAE

1A. Color uniform black or dark brown except for lighter or darker fins in some species ..... *Apristurus*

1B. Color variegated with spots, blotches or saddles, lighter below ..... 2A or 2B

2A. Crest of enlarged denticles along upper edge of caudal fin ..... *Galeus*

2B. No crest of enlarged denticles along upper edge of caudal fin ..... 3A or 3B

3A. Tip of snout to anus about one-third of total length ..... *Schroederichthys*

3B. Tip of snout to anus about three-eighths to one-half of total length ..... 4A or 4B

4A. Labial fold present only along lower jaw ..... *Scyliorhinus*

4B. Labial fold around corner of mouth extending along both jaws ..... *Halaelurus*

Genus *Scyliorhinus* Blainville 1816

Type species—*Squalus canicula* Lacépède, designated by Gill, 1861.

Western Atlantic species of *Scyliorhinus* differ from one another primarily in color pattern although one species, *Scyliorhinus torrei*, is much smaller than the other four and another, *S. meadi*, has more erect and slightly larger denticles than any of the others, giving it a somewhat shaggy appearance.

Scyliorhinus torazame (Tanaka) [=*Halaelurus rudis* (Pietchmann)] of Japanese waters, *S. stellaris* (Linnaeus) and *S. canicula* (Linnaeus) of eastern North Atlantic waters, and *S. capensis* (Müller and Henle) of South Africa and the eastern Indian Ocean, all differ in details of color pattern from one another and from American species. No eastern Pacific species are known. Specimens of *S. torazame* that have been examined have the pelvic fins united to a point somewhat nearer their tips than most specimens of the American species and have enlarged and nearly erect dorsal denticles rather regularly scattered on dorsal surfaces among more numerous smaller ones; but the larger denticles are not arranged in rows, and the character seems to be variable. The American species, excepting *S. torrei*, have slightly longer snouts than other species. The European *S. canicula* has the two nasal flaps united at the midline, and the confluent flap reaches the edge of the upper lip. As for other members of the genus, nasal flaps are often smaller in examples of the American species than in others, but specimens can be selected from series of *S. stellaris* and *S. retifer*, for example, in

TABLE 2.—*Characteristics of genera of the family Scyliorhinidae as present in western Atlantic species*

Characters	*Scyliorhinus*	*Halaelurus* (shortest snout)	*Galeus*	*Schroederichthys*	*Apristurus* (longest snout)
Color	Variegated; dorsal saddles present but sometimes obscure.	As in *Scyliorhinus*	Plain color or variegated but without well-marked saddles.	As in *Scyliorhinus*	Black or sometimes brown; color uniform without strong markings.
Caudal crest	None	None	Present	None	Absent except partly developed in one species.
Labial grooves	Weak; present only on lower jaw.	Strong on both jaws	Moderate on both jaws	Moderate on both jaws	Strong on both jaws.
Union of pelvic fins posterior to anus.	About two-thirds united.	Basal one-fourth to one-half united.	Basal one-half to two-thirds united.	No union	Only trace of union.
Enlarged dorsal denticles.	Present in embryos; and scars in very young.	A few remain in some adults.	Few scars on very young.	Not found on material available.	Not found.
Claspers	Short; hooks weak or absent.	Not examined	Long; hooks present	Long; no hooks	Short; no hooks.
Clasper siphons	Moderately short	Not examined	Moderately long	Long	Short.
Egg retention	Oviparous as far as known.	Oviparous as far as known.	Both oviparous and ovoviviparous species.	Oviparous as far as known (in 1 species).	Oviparous as far as known (in 2 species).
Sexual dimorphism in tooth shape.	Not found	Said to be present to slight degree.	Not found	Not found	Strong tooth dimorphism in 1 species, not in 3 others.
Pores on snout	Not prominent	Not prominent	Prominent	Not prominent	Very prominent.
Liver size in adults	Large; posterior tips usually reach as far back as anal opening.	Not examined	Moderate; posterior tips of liver lobes not reaching as far back as anus.	Short; small; not extending appreciably into posterior half of body cavity.	Large; very long; tips reaching posterior to anus.

which there are no appreciable differences in the shape of the nasal flap or its nearness to the mouth.

Thus throughout the genus *Scyliorhinus*, excepting only *S. canicula* where the nasal flaps do provide a structural feature differing from that found in all other species, the best and by far the most reliable character for identification of specimens is their color pattern. Differences in proportions do exist, and there are other differences in denticle and tooth structure and in the shape and position of fins; but these differences seem to be of little practical usefulness at this stage of the study of the family except in the analysis of series of specimens and in preliminary determinations of probable relationships.

KEY TO WESTERN ATLANTIC *SCYLIORHINUS*

Note.—Preservatives dissolve oil from shark livers, adding yellowish pigments to specimens, sometimes turning gray colored specimens to brown.

1a. Dorsal surfaces (except fins) with randomly arranged but almost uniformly spaced, light-colored and nearly round spots in a brown background (brown in life as well as in preservative); darker areas representing seven saddles may be present but are usually obscure; lighter below, without spots.

S. torrei; Florida Straits, off northern coast of Cuba.

1b. Dorsal surfaces neither brown in life (but may be brown in preservative) nor covered by randomly arranged white spots; all species with variations on a basic pattern of seven saddles, a prepectoral, a pectoral, postpectoral, first dorsal, second dorsal, precaudal, and caudal saddles; additional darker areas (blotches or saddles) may occasionally appear in intermediate positions such as between the dorsal fins, but such blotches or saddles are usually more obscure than the seven principal saddles; lateral pattern, when present, sometimes with a series of blotches roughly alternating with saddles.

2a. Saddles made up of simple blotches of darker color, usually without included darker lines or darker spots; lighter areas within saddles sometimes present but rather indistinct, not appearing as round whitish spots smaller than diameter of eye; intermediate saddles and spots outside basic pattern few or absent.

S. meadi new species; Florida Straits, St. Augustine to Santaren Channel.

2b. Saddles and lateral blotches with nearly round, white or light-colored spots included within their margins, these spots usually smaller than diameter of eye; no dark lines or dark spots within the saddles; some specimens with reduced number of saddles.

S. hesperius new species; western Caribbean, off Honduras, Nicaragua, and Jamaica.

2c. Dorsal saddles with black marginal lines enclosing areas of the lighter background color, the enclosed areas usually not round, in most specimens the lines forming a reticulate pattern; the reticulate pattern commonly extended to form intermediate patterns obscuring basic pattern of saddles, but in a few specimens reduced and showing only as saddles with marginal lines but without reticulating lines (fig. 2A and 2B show patterns near extremes of variation in material examined); no round white spots and isolated black spots few.

S. retifer (Garman); southwestern edge of Georges Bank (New England) along the outer continental shelf and the continental slope to the Carolinas and along the continental slope southward; off both east and west coasts of Florida; along the continental slope in the Gulf of Mexico and the western side of the Yucatan Channel; present on western Caribbean Banks including Pedro Bank as far south as Latitude 13°30′ N. Not yet reported from Cuba or the Antillean side of the Straits of Florida.

2d. Pattern of saddles usually outlined by small rounded black spots which may be present also outside the pattern; in some specimens black spots are so numerous as to obscure saddles; no white spots.

S. boa (Goode and Bean); Lesser Antilles and continental slopes of South America from Venezuela to northern Argentina.

Scyliorhinus torrei Howell-Rivero, 1936

Figures 4, 7, 14, and 27; tables 1, 3, and 4.

Scyliorhinus torrei Howell-Rivero, Proc. Boston Soc. Natur. Hist. 41(4): 43–44, pl. 9, 1936 (type locality off Havana in deep water).

S. torrei is the smallest species of the genus, the males becoming mature at about 250 mm. In this connection it should be noted that Ford (1921) finds no marked difference in sizes attained by males and females in *Scyliorhinus canicula* and that the series of all scyliorhinids examined in this study show no indication that there is a disparity in size attained by the sexes. The numbers of adult specimens examined, however, are too few to show this conclusively for any western Atlantic species. The largest specimen of *S. torrei* recorded is 209 mm. (Bigelow and Schroeder 1948). As might be expected from its small size and slender form, *S. torrei* has a short liver occupying only a part of the anterior half of the body cavity. Proportionally large ovarian eggs (in the right ovary in adult females) with diameters up to 10 mm. crowd other organs. In gross appearance the nidamental gland and oviducts in *S. torrei* are

much the same as in other western Atlantic scyliorhinids, but it is not known whether *S. torrei* is oviparous or ovoviviparous.

Howell-Rivero (1936) in describing *S. torrei* noted the presence of a nictitating membrane and by this (among other characters) distinguished it from *S. torazame* of Japanese waters. Among specimens of both species examined for this study there is some difference in the degree of development of the subocular fold. Gilbert and Oren (1964) have called attention to inconsistencies in use of the terms subocular fold and nictitating membrane or nictitans, and I follow their recommendation in restricting the meaning of subocular fold to indicate a poorly developed lower eyelid. The presence of a nictitans or its state of development has sometimes been assumed from the presence of a subocular fold or its length relative to the length of the eye. Although there are differences in the extent of development of the subocular fold in different species, there is also much variation within species apparent in museum specimens, some of it due to differences in methods of preservation. Winking by the nictitans was observed in the two European *Scyliorhinus* Gilbert (1963), but its functional movement has not been observed and reported for other scyliorhinids.

In males the extent of union of pelvic fins along their inner edges is variable in the material examined. In one immature male the inner edges are united throughout, and one adult male has fins that are not united at all. Other males examined have fins united along two-thirds to three-fourths of their inner margins. Bigelow and Schroeder (1948) state that male *S. torrei* have claspers extending far beyond the tips of the pelvics. The illustration (1948, fig. 35), however, shows that the claspers of their largest specimen reach only a short distance beyond the pelvic tips. In the material at hand, the fully calcified claspers of one adult male (the largest) fail to reach the tips of the pelvics. In two others the claspers extend a very short distance beyond the tips of the pelvics. The ventral (outer) surfaces of the claspers, in the unflexed condition, are covered with denticles except for the extreme tip. Denticle points are directed anteriorly (toward the clasper base) as in other sharks of the suborder Galeoidea. The inner surface does not have either denticles or hooks in the position indicated by Schmidt (1930) for hooks on claspers of *Scyliorhinus torazame* (Tanaka). On the adult male *S. torrei* at hand, there are somewhat irregular series of slightly enlarged denticles having sharp points directed ante-

FIGURE 14.—A, *Scyliorhinus torrei* Howell-Rivero, drawn from a 258-mm. adult female collected at M/V *Silver Bay* station 2457; B, *Scyliorhinus meadi* new species, drawn from a 190-mm. young male taken at M/V *Combat* station 51.

riorly (toward the base of the clasper), but these denticles are on the side of the rhipidion adjacent to the main axis of the shark and in quite a different poistion than the hooks of the claspers of *S. torazame*.

The claspers of *S. torrei* are quite small and simple structures as compared with the claspers of *Galeus area*. The claspers of an adult male *Galeus arae* 275 mm. long are obviously more than 10 times the weight or volume of the claspers of an adult male *Scyliorhinus torrei* 272 mm. long and are considerably more complicated.

The stomach on one *S. torrei* contained cephalopod remains (beaks) including a cartilaginous eye capsule (*Sepia?*) 12 mm. in minimum diameter. Also present were several fish scales 4 to 7 mm. in breadth.

In addition to specimens for which measurements are summarized in table 4 (M/V *Silver Bay* stations 2457 and 3474 in Santaren Channel), specimens have been seen from M/V *Silver Bay* stations 2475 and 2477 in Santaren Channel; from M/V *Oregon* stations 1340 and 1343, also in the Santaren Channel; from M/V *Oregon* stations 2482, 3474, and 3512, northward from the Santaren Channel to the offing of Jupiter, Florida; and from M/V *Oregon* station 2650, near the Virgin Islands. Previously recorded specimens were from the north coast of Cuba (Bigelow and Schroeder, 1948). All recorded captures were from 366 to 550 m. except the one near the Virgin Islands which was in 229 m.

The teeth in the specimens at hand are in 21+21/20+2+20 to 23+23/21+1+21 rows. The tooth shape is similar to that of other Atlantic species of *Scyliorhinus*. In the specimens examined, the cusps of the extreme lateral teeth of the lower jaw are variably reduced, in some almost absent.

Scyliorhinus meadi new species

Figures 3, 7, 14, and 27; tables 1, 3, and 4.

Holotype.—An immature male, USNM 188049, 247 mm. in total length, taken at M/V *Silver Bay* station 3711, lat. 28°21′ N., long. 78°51′ W., at 329-m. depth off Cape Kennedy, Fla., January 26, 1962.

Additional material examined. The species is known only from the holotype, an immature male and two immature females from the same station as the holotype, an immature male from M/V *Silver Bay* station 2475 from 549-m. depth in Santaren Channel, and an immature male from M/V *Combat* station 51, off St. Augustine, Fla. in 329-m. depth.

Diagnosis.—*S. meadi* differs from other species of the genus *Scyliorhinus* in color pattern. The upper parts are light gray in fresh specimens (brownish in specimens preserved in alcohol) with seven quite distinct darker rectangular blotches or saddles extending across the middorsal area, the first anterior to the pectorals, the second and largest (in specimens of the type series) at the level of the pectoral tips, the third anterior to the pelvic origin, the fourth through the first dorsal fin, the fifth through the second dorsal fin, the sixth at the base of the caudal fin, and the seventh across the caudal fin, anterior to the notch. In additional to the dorsal saddles, a series of lateral blotches of color alternate in more or less checkerboard fashion with the first three or four dorsal saddles, some of these extending indistinctly to the upper surfaces of the pectoral and pelvic fins. Traces of additional dorsal blotches are present between some of the principal dorsal saddles in some of the specimens. Lighter colored areas are included in some of the blotches, but these are indistinct and larger than the eye.

Two species of *Scyliorhinus*, *torrei* and *retifer*, are present in the same geographical area as *meadi*, but the color patterns of these are so strikingly different from that of *meadi* that there should not be any possibility for confusing them. No intergrades have been observed.

S. meadi appears to be closest in appearance to *S. hesperius* which is described in the following pages. Differences in color pattern between the two are constant in the material examined.

S. meadi also differs from other American members of *Scyliorhinus* in having the typical dermal denticles of dorsolateral surfaces somewhat larger in comparison with specimens of equal size, somewhat more erect, somewhat narrower, and somewhat more widely spaced. These differences are all a matter of degree and are not necessarily apparent unless specimens of similar size are compared. The differences do, in combination, give *S. meadi* a more shaggy appearance than any of the other American representatives of the genus.

Description of holotype.—An immature male, 247 mm. in total length and having dimensions as given in table 3. Body robust, caudal axis little elevated; head broad; snout broadly rounded, short; nasal flaps rather large, separated from one

another in the midline, nearly reaching mouth, no groove connecting nasal apertures with mouth; mouth broad, strongly arched; well-developed labial folds along the inner sides of the jaws extending about one-fourth the distance toward the symphysis, no labial folds along outer margins of jaws; orbital opening elongate, slitlike, a well-developed fold below the eye, not touching eyeball; spiracle small, its diameter less than one-fifth length of eye, located slightly below level of eye and at a distance about one-third the eye's longitudinal diameter from corner of eye; third gill slit above origin of pectoral, fourth, and fifth gill slits over pectoral; first dorsal fin slightly larger than second, its origin over the posterior half of base of pelvics and slightly nearer tip of snout than tip of caudal fin; pelvic fins united along their inner margins for about half the distance from cloaca to fin tips; pectorals broad, their free corners rounded, distal margins nearly straight.

Bases of typical denticles of dorsolateral surfaces separated from one another by distances one to four times the diameter of their bases; denticles three pointed, the central point long and heavy, lateral points weak and quite small with a strong central ridge, most denticles nearly erect, much longer than wide, their points directed upward and posteriorly; belly denticles similar; a few denticles of the edges of fins flattened, leaf-like, and without lateral points.

Teeth similar in the upper and lower jaws, three-cusped with an additional pair of lateral denticles on some teeth; the central cusp of teeth of the midportion of the upper jaw about twice as high as lateral cusps; teeth toward the angles of both jaws and in the lower jaw with somewhat lower central cusps; about three series of teeth functional, in about 25+0+25/25+0+25 rows.

Color pattern as described in preceding key and diagnosis.

Notes.—*S. meadi* specimens were collected within the general geographical range of *S. retifer* and adjacent to the areas in which *S. torrei* have been found. It is possible that all three species occupy different habitats. Species of *Scyliorhinus* taken by exploratory fishing vessels off the southeastern States and in the Caribbean have been, with one exception, collected from depths between 180 and 914 m. Along much of the Atlantic coast this is a relatively narrow strip (fig. 1). In the Florida Straits region, a wider band of sea-bottom falls within this depth range and supports a remarkably diverse fauna of sharks and rays. Collections in the area in general suggest that many of these have quite restricted distributions, possibly due to narrow habitat preferences.

S. meadi is named for Giles W. Mead, who first called my attention to a specimen of the species.

Scyliorhinus boa Goode and Bean, 1896

Figures 15 and 27; tables 1, 3, and 4

Scylliorhinus boa Goode and Bean, Spec. Bull. U.S. Nat. Mus., p. 17, 1896 (type locality, *Blake* station 291, off Barbados).

Catalus haeckelii Miranda-Ribeiro, Mem. Mus. Nac. Rio de Janeiro, 14:163, pl. 8, 1907.

Scyliorhinus fernandezi Weibezahn, Novedades Cient. Mus. Hist. Nat. La Salle, Caracas, Ser. Zool. No. 9: 3–7, 1953.

Goode and Bean (1896, p. 17) did not intend to describe the species but did, in fact, satisfy the requirements of a valid description by publishing a name and a diagnosis based on the single 6-inch specimen collected off Barbados which is the type (Harv. Mus. Comp. Zool., 1335). They note a general correspondence in color with *S. retifer* and state that in approximately the track of the narrow lines observable in Garman's specimen (*S. retifer*) may be found various spots and blotches of blackish-brown. The similarity to a basic color pattern in each of the Atlantic American species has been mentioned. In the 14 specimens of *S. boa* examined and reported in table 3 and a few other specimens that have been examined, the color pattern is consistent in the absence either of the reticulating black lines or of continuous unbroken black lines around saddles that characterize specimens of *S. retifer* at all ages. Also none of the specimens of *S. boa* examined have white spots in the saddles as do all of the specimens of *S. hesperius* examined.

The pattern of spots in *S. boa*, however, does vary considerably. The dorsal saddles or their outlines are obscure in one specimen, and small black spots are quite numerous and randomly distributed over the dorsal and lateral surfaces. In most of the specimens the saddles and lateral blotches are outlined by discrete black spots, more or less round and much smaller than the eye. The spots extend on to the upper surfaces of the pectoral and pelvic and are present on the dorsal

fins and on both the upper and lower lobes of the caudal fin.

Species described as *Catulus haeckelii* Miranda-Ribeiro, 1907, and as *Scyliorhinus fernandezi* Weibezahn, 1953, are regarded here as being synonymous with *S. boa*. The geographical range of *S. boa* extends at least from the continental slope of central Venezuela eastward and southward to Rio de Janeiro where it was taken by Miranda-Ribeiro (1907). Dr. Elvira M. Siccardi has told me (personal communication) of the presence of *S. boa* or a closely allied population off the northerly coast of Argentina. A photograph of one specimen shows somewhat longer and larger black spots than characterize the specimens seen from Venezuela and the Guianas. Whether the juvenile specimen reported by Bigelow and Schroeder (1948) from the north coast of Cuba is correctly identified as *S. boa* now appears questionable. Material examined in this study in addition to the type is from 10 stations of the M/V *Oregon* off the coasts of Venezuela, the Guianas, and Brazil, from lat. 11°34′ N., long. 62°52′ W., to lat. 01°52′ N., long. 46°54′ W., in 293 to 402 m.

The teeth in *S. boa* in specimens examined were from 24+24/21+1+21 to 25+25/23+1+23. The teeth were somewhat smaller than the teeth of other western Atlantic *Scyliorhinus* of similar size. Also the central cusps are comparatively shorter, and nearly all teeth have five cusps, with only teeth of the central part of the upper jaw having the middle cusp of each tooth twice as long as the cusps next to it.

The dermal denticles of the dorsolateral surfaces differ from the denticles of *S. meadi* in being smaller, wider (some of them nearly as wide as long), set closer together, and less erect. The denticles of *S. boa* differ very little from denticles of other Atlantic American members of the genus. Denticle differences due to age and perhaps also to intraspecific variation are so great, however, that these are probably not ordinarily useful in identifying material.

S. boa seems to be a smaller species than *S. retifer* or *S. hesperius*, since a 346 mm. male is sexually mature. The claspers of this male reach 4 mm. past the tips of the pelvics which are united to one another along their inner margins to within 6 mm. of their tips. The claspers are not provided with hooks but have a few slightly enlarged denticles which have points directed anteriorly (toward the base of the claspers) as in the denticle arrangement on claspers of all galeoid sharks.

Scyliorhinus retifer (Garman), 1881

Figures 2, 5, 6, 7, 8, and 27 ; tables 1, 3, and 4

Scyllium retiferum Garman, Bull. Mus. Comp. Zool. 8:233, 1881 (type locality, lat. 38°23′ N., long 73°34′ W.).

This species is easily recognized by its unique pattern of reticulating lines sometimes reduced to black edging lines along margins of saddles and blotches. It is the only Atlantic American catshark known well enough to have acquired an English common name, the chain dogfish. It is frequently taken by trawlers operating off the Virginia Capes.

The known range of the species extends from the offing of southern New England and the southwestern edge of Georges Bank to Nicaragua. Bigelow, Schroeder, and Springer (1953) note that it has been taken at depths of 73 to 229 m. in the northern part of its range. Specimens of *S. retifer* have been seen from more than 100 stations of Bureau of Commercial Fisheries Exploratory Fishing vessels between the Virginia Capes, the lower Gulf of Campeche, and off central Nicaragua (lat. 13°30′ N., long. 82°00′ W.), along the continental slope. The station with the least depth was at 165 m. off Cape Henry, Va., where over 500 juveniles about 160 to 200 mm. long were taken in early May, 1961. Southward the collections were at greater depths, for the most part from 330 to 450 m. off Florida and in the Gulf of Mexico, but 500 to 550 m. off Nicaragua. One specimen of *S. retifer* was taken from M/V *Oregon* station 1883 on the continental slope off Honduras at 365 m. where a specimen of *S. hesperius* was also taken. Southward from this station along the continental slope for a distance of about 200 miles, where the two forms occupy adjacent or nearly overlapping ranges, *S. retifer* was taken in an average depth of 525 m. (460 to 550 m.) at 16 stations, while *S. hesperius* was taken at an average depth of 400 m. (274 to 530 m.) at 7 stations.

A peculiarity of the distribution of *S. retifer* is that records of it occurrence on the Antillean side of the Straits of Florida (off Cuba and the Bahama Banks) are absent. *S. torrei* records are chiefly from this area, and one of the three sta-

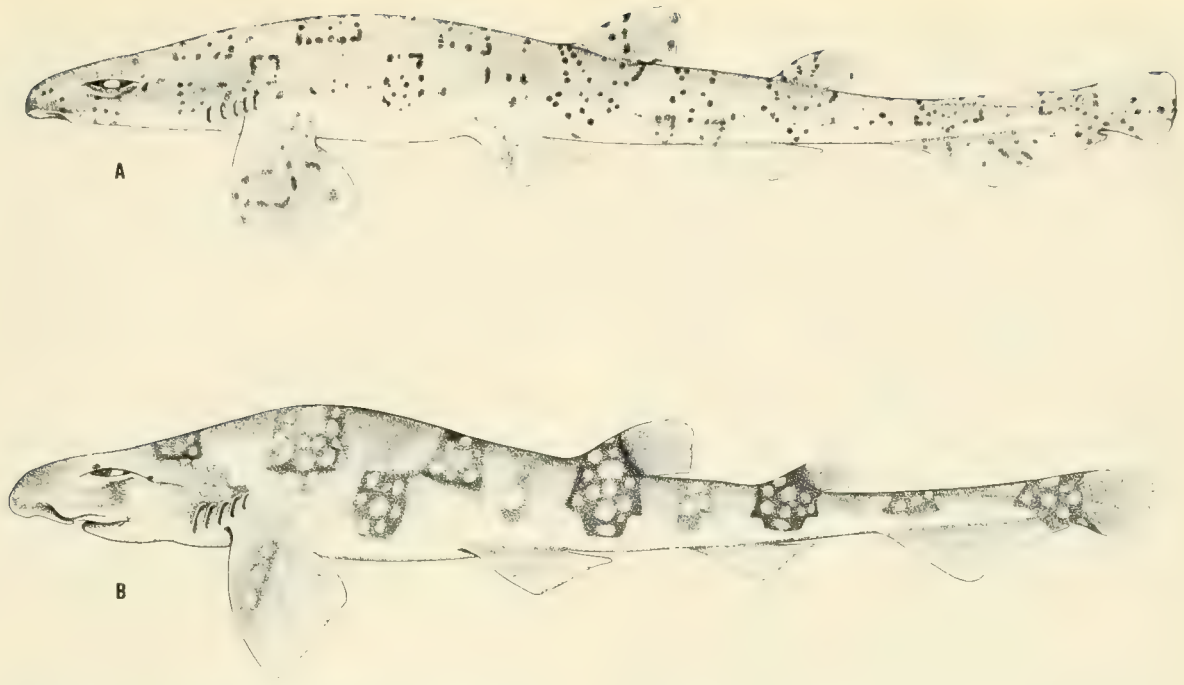

FIGURE 15.—A, *Scyliorhinus boa* (Goode and Bean) drawn from a 348-mm. female from M/V *Oregon* station 2351; B, *Scyliorhinus hesperius* new species, drawn from a 260-mm. female from M/V *Oregon* station 1883.

tions where *S. meadi* was taken is close to the Bahama Banks.

Despite the extensive collection of *S. retifer* available for study, few of the specimens are adults. A male, 395 mm. in total length, taken by the Bureau of Commercial Fisheries M/V *Delaware* in 128 m. off Delaware Bay, was the only specimen observed that was determined to be sexually mature.

A 475-mm. female taken from 402 m. off Pensacola, Fla., was the largest specimen examined. The ovary was extremely small, without evidence of developing eggs.

The stomach of the 475-mm. specimen contained 12 cephalopod beaks of more than one type.

Teeth of specimens of *S. retifer* are in 21+21/19+2+19 to 26+26/21+4+21 in specimens examined. In form, the teeth of *retifer* do not differ greatly or consistently from teeth of other Atlantic American species of *Scyliorhinus*.

Scyliorhinus hesperius new species

Figures 7, 9, 15, and 27; tables 1, 3, and 4.

Holotype.—An immature female, USNM 187732, 415 mm. in total length, taken at M/V *Oregon* station 3598, lat. 09°03′ N., long. 81°22′ W., at 360- to 400-m. depth on the Caribbean coast of western Panama, May 31, 1962.

Additional material examined. Twelve specimens, 177 to 466 mm. total length, taken at M/V *Oregon* stations 1870, 1883, 3522, 3565, 3574, 3575, 3598, 3599, 3626, 4480, and 4482, all in the western Caribbean from the vicinity of Jamaica and Honduras, southward to Panama and off Barranquilla, Columbia, in 274- to 530-m. depth.

Diagnosis.—*S. hesperius* resembles *S. boa*, *S. meadi*, and *S. retifer* in proportions and external structural features but differs from these species in having from 2 to about 35 round white spots, smaller than the diameter of the eye, within each of the dorsal saddles and lateral blotches. The species differs from *S. retifer* in the absence of reticulating lines or in the absence of darker margins around the saddles and blotches. It differs from *S. boa* in the absence of small black markings either scattered or outlining the saddles and blotches. The presence of small white spots in *S. hesperius* separates it from *S. meadi* in all the specimens seen. The white spots in *S. hesperius* are concentrated in the saddles and blotches and are not more or less randomly distributed as in *S. torrei*.

Description of holotype.—An immature female, 415 mm. in total length and having dimensions as

given in table 3. Body robust, caudal axis not elevated; head broad; snout broadly rounded, short; nasal flaps rather large, each with a central swelling dividing each flap into two portions which cover the two parts of each nasal aperture, separated from one another in the midline, nearly reaching mouth, no groove connecting nasal apertures with mouth; mouth broad, moderately arched; well-developed labial folds extending a short distance along the inner sides of lower jaws, no labial folds along outer margin of upper jaws; orbital opening elongate, slitlike, a well-developed fold below eye, not touching eyeball; spiracle small, located short distance from rear corner of eye, about same level as eye; fourth and fifth gill slits over pectoral base; first dorsal origin over end of base of pelvics, its area about twice that of second dorsal; second dorsal origin slightly in advance of posterior end of anal fin base; anal fin origin very slightly posterior to free tip of first dorsal, its free tip reaching end of base of second dorsal; caudal fin less than one-fourth total length; pectoral fins broad, short, their distal margins nearly straight; pelvic fins united along their inner margins about half the distance from anus to fin tips.

Denticles, three-ridged, imbricate, with a single strong apical (posterior) point with a weak lateral point on each side, denticle size not uniform, some twice as large as others.

Teeth similar in upper and lower jaws, small, in 24+0+24/22+2+22 rows; each tooth with 3 or more smooth-edged cusps, the central cusp longest, most teeth with two pairs of lateral cusps, the outer pair very small.

Color pattern of type approximately as illustrated for specimen shown in figure 15B.

Schroederichthys new genus

Type species—*Schroederichthys maculatus* n. sp.

Members of this genus differ from nearly all other sharks in having the postpelvic trunk region in advance of the caudal fin greatly elongated, the distance from the origin of the pelvics to the origin of the caudal fin lobes about one and three-fourths times the distance from the tip of the snout to the origin of the pelvics. In this character of body proportions, members of the genus *Schroederichthys* show a parallel development with some Australian sharks of the family Orectolobidae, particularly *Hemiscyllium*. These orectolobids, however, have quite different arrangements of parts near the mouth and have nasoral grooves and barbellike structures. In *Schroederichthys* also the anal fin is separated from the lower caudal lobe by a considerable distance (a distance equal to about two times the length of the base of the anal), whereas in some orectolobids (*Hemiscyllium* and related genera) only a notch separates the anal from the lower caudal lobe.

Schroederichthys differs from *Scyliorhinus* in having definite though short labial grooves along both upper and lower jaws at the corners of the mouth. It is similar to the two Chilean-Patagonian species provisionally referred to the genus *Halaelurus* in having upper labial grooves or folds. *Schroederichthys* differs from these species in having a somewhat longer postpelvic trunk, shorter labial grooves, and consistently (at all ages in *S. maculatus*) multicusped teeth in both jaws.

Generic description.—Small slender sharks of the family Scyliorhinidae having greatly elongated caudal regions with relatively short caudal fins; distance from tip of snout to vent about half the distance from vent to tip of tail; caudal axis little elevated, lower caudal fin not produced as a lobe; two dorsal fins, second dorsal slightly larger than first and similar in shape, first originating behind posterior end of pelvic base; anal fin relatively low, its base longer than base of either dorsal fin; pectoral fins relatively broad, their distal margins straight or very slightly convex, their outer corners rounded; pelvic fins with their inner-posterior corners somewhat produced and their distal margins oblique, pelvics of males united at bases for a very short distance, not forming an apron.

Snout only moderately rounded; nasal flaps small but extending across the nasal apertures; nostrils not united with mouth by a groove and separated from mouth by a distance as great as or greater than width of nasal flap; mouth strongly arched; labial grooves short but extending around corners of mouth; eye elongate, with well-marked fold below, not in contact with eye; spiracle small, on level of eye and close behind it; gill slits five, anterior longest, two posterior slits over pectoral base; no ridges or keels in skin, no precaudal pits, a shallow groove on midventral line posterior to

pelvics and extending, interrupted by anal fin, nearly to lower caudal fin.

Teeth similar in upper and lower jaws (fig. 9), principal ones with three or five cusps, central cusp of each tooth much the longest, three to five series functional. Dorsolateral denticles (fig. 7F) for the most part imbricate, three pointed, the central posteriorly directed point much the longest, ventral denticles leaf-shaped, with a single point.

Vertebrae (in 36 specimens) 132 to 142, monospondylous vertebrae 29 to 35.

Type species oviparous, eggshells (fig. 19) with rather thick walls, their surfaces striated longitudinally, opaque, about 44 mm. by 14 mm., not including tendrils developed at the four corners.

Claspers of adult males of type species long, extending well beyond tips of pelvics, their tips tapered, without hooks; clasper siphons very large, long, extending under skin of belly as far forward as axils of pectorals.

Livers relatively small, occupying only the anterior half of body cavity in adults.

General pattern of seven dorsal saddles of darker color showing at least in young; sometimes obscure in adults in the type species.

The genus is named for William C. Schroeder, whose careful and pioneering work with Henry B. Bigelow on cartilaginous fishes contributed greatly to a renewal of interest in problems relating to this important group of marine animals.

Schroederichthys maculatus new species

Figures 4, 5, 7, 9, 16, 17, and 19; tables 1, 5, and 6.

Holotype.—Adult male 328 mm. total length, USNM 185556, collected in shrimp trawl at R/V *Oregon* station 1870, August 21, 1957, from about 410 m.; lat. 16°39′ N., long. 82°29′ W., in the Caribbean sea NNW of Cape Gracias a Dios, Honduras.

Paratype.—An adult female 335 mm. in total length, taken in the same haul with the holotype.

Diagnosis.—*Schroederichthys maculatus* is readily distinguished from sharks of all other genera by the proportionately greater length of the tail region. It differs from the other species of *Schroederichthys* described in this paper in color, in the shape of the nasal flap, which in *S. maculatus* is triangular with a somewhat bilobed distal margin as compared to the narrower, longer flap with a simple rounded tip of the other species. The color differences are so great between the two species of *Schroederichthys* that other differences are of comparatively little interest for practical identification of the two forms. *S. maculatus* has a color pattern almost identical with that of *Scyliorhinus torrei* Howell-Rivero. The dorsal surfaces are tan or light brown with round, ovoid, or irregularly shaped white or cream-colored spots about 1 to 3 mm. in diameter scattered over the dorsal surfaces except on the surfaces of the dorsal

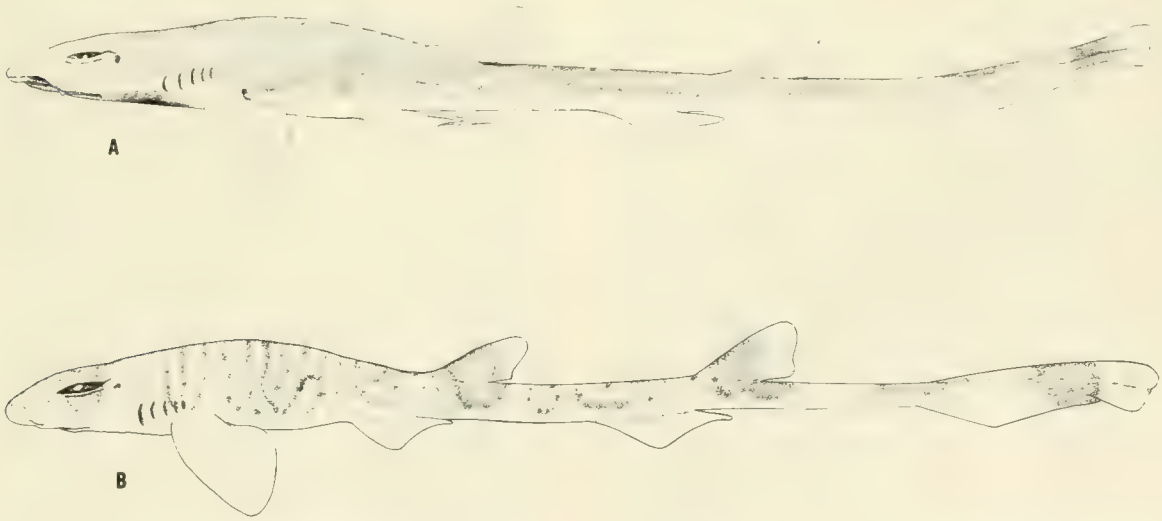

FIGURE 16.—A, *Schroederichthys maculatus* new species, drawn from the type, USNM 185556, a 328-mm. adult male; B, *Schroederichthys tenuis* new species, drawn from the type, USNM 188052, a 230-mm. immature male.

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fins and the paired fins, and with traces of 10 dorsal saddles appearing as areas of somewhat intensified brown color; these saddles are obscure or absent anteriorly in some adults. This color pattern is so close to that of *Scyliorhinus torrei* that specimens in a mixed lot of the two species are not readily distinguishable from one another on the basis of color. The other species of *Schroederichthys* resembles *Scyliorhinus boa* in general coloration, having a pattern of dark spots spots and lines on a lighter background.

Description of the holotype.—The holotype is shown in figure 16A, and measurements are given in table 5. Teeth in 24+2+24/(18+)+2+(18+) rows; most of them tricuspid but some with additional small lateral cusps; largest upper jaw teeth about 0.9 mm. high by 0.7 mm. in greatest width, central cusp projecting beyond base about five times length of lateral cusps, edges of cusps smooth, six or more low surface ridges extending from bases about half-way toward tips of cusps; lower jaw teeth similar but central cusps somewhat lower, length of central cusp of largest tooth about four times height of lateral cusps, surface ridges very short, present only on lower portion of the bases.

Typical denticles of dorsalateral surfaces about 0.4 mm. long by about 0.2 mm. wide, with three points directed upward and posteriorly, central point much the longest, not very close set, with skin surface showing around each denticle but points overlapping, imbricate.

Color of dorsolateral surfaces of body light brown with numerous round or oval spots of lighter color, about half the length of the eye or smaller and irregularly scattered; darker brown dorsal saddles without definite darker edging present but obscure anteriorly and extending to fins only as a trace of darker color; no definite spots on fins; ventral surfaces white, unmarked.

Notes.—*Schroederichthys maculatus* is known from 48 specimens, all from the Caribbean continental slope of Central America off Honduras and Nicaragua. The specimens were collected from depths of 190 to 410 m., most of them near Rosalind Bank and Quita Sueño Bank. The capture of more than 30 specimens in one net haul suggests that the species is locally abundant.

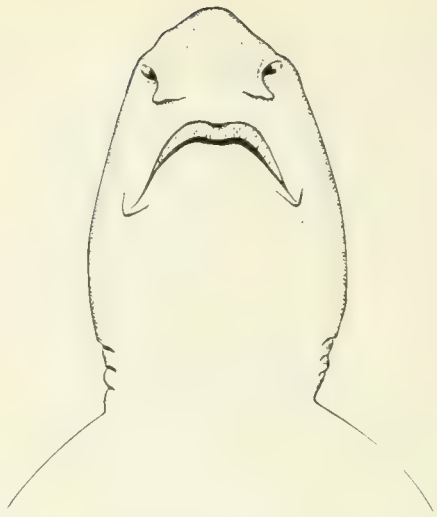

FIGURE 17.—*Schroederichthys maculatus* new species, ventral side of head of the type, USNM 185556.

Schroederichthys tenuis new species

Figures 16 and 18; tables 1, 5, and 6.

Holotype.—An immature male 230 mm. in total length, USNM 188052, collected in a shrimp trawl at M/V *Oregon* station 2083 on November 17, 1957, from about 410 m. at lat. 01°49′ N., long. 46°48′ W., in the Atlantic off the mouth of the Amazon River.

Paratype.—An immature male 180 mm. long, USNM 188053, taken in the same haul with the holotype.

Diagnosis.—*Schroederichthys tenuis* is known only from the types, both immature males. There appear to be no important differences in body proportions between these specimens and specimens of *S. maculatus* of comparable size. *S. tenuis* is, of course, readily separable from sharks of other genera. From *S. maculatus*, it differs greatly in color pattern. In addition, *S. tenuis* has a nasal flap longer than wide, and its tip is simply rounded, not pointed or bilobed. The typical dermal denticles of dorsal surfaces in *S. tenuis* are proportionally somewhat narrower than in *S. maculatus* and more erect. Some have three posteriorly directed points, but many of them lack lateral points and are needlelike, although usually showing a central ridge. The color pattern of *S. tenuis* is made up of dark spots on a lighter ground color, the spots assembled to form a series of dorsal saddles.

Description of holotype.—The holotype is shown in figure 16B and measurements are given

in table 5. Teeth in 22+22/16+2+16 rows, about half with three cusps and half with five cusps. Color of dorsolateral surfaces light brown without lighter colored spots or markings; pattern of seven dorsal saddles plus several more or less distinct intermediate saddles edged with broken lines of darker color, saddles at the first dorsal and second dorsal fins more intense and extending across the fins, caudal fin strongly marked, paired fins and anal fin only faintly marked.

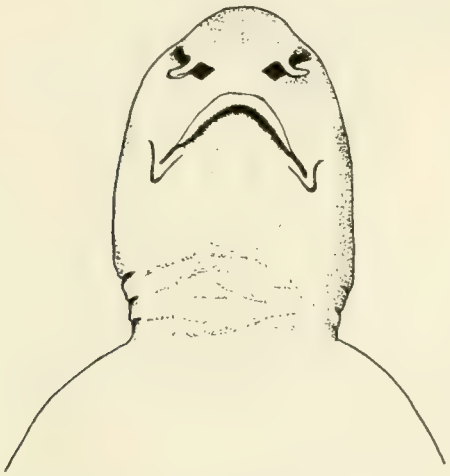

FIGURE 18.—*Schroederichthys tenuis* new species, ventral side of head of the type, USNM 188052.

Notes.—The collection of only two specimens of this species nearly 2,000 miles from the area from which *S. maculatus* is known illustrates the incompleteness of the sampling of the fauna from continental slopes.

Genus *Galeus* Rafinesque, 1810

Type species—*Galeus melastomus* Rafinesque, designated by Fowler, 1908.

Galeus is a genus with about eight nominal species, one of which, *Galeus melastomus* Rafinesque, of the eastern North Atlantic region, is well known. Members of the genus are characterized by the presence of a spiny crest of enlarged denticles on the upper margin of the caudal fin (fig. 21) and a comparatively long snout. An Australian scyliorhinid with enlarged denticles forming crests along both the upper margin of the upper caudal lobe and the anterior margin of the lower caudal lobe has been split off from *Galeus*

FIGURE 19.—Partially formed egg case of *Schroederichthys maculatus* taken from an oviduct of a 342-mm. female collected at M/V *Oregon* station 1870, August 21, 1957. The egg case was 44 mm. long by 14 mm. in greatest width, and the posterior tendrils (broken off in drawing) were 225 mm. long. The anterior end of the egg case was still within the nidamental gland area when taken, and anterior tendrils had not formed. The egg case wall was rather thick, opaque, olive colored, and striated longitudinally.

under the name *Figaro boardmani* (Whitley). A group of two Pacific scyliorhinid species, *Parmaturus xaniurus* (Gilbert) and *P. pilosus* Garman, have crests with specialized denticles along the upper margin of the caudal fin, but these crests extend somewhat onto the lateral surface of the upper caudal lobe, and the marginal scales, although enlarged, do not project outward from the tail to the degree characteristic of these scales in *Galeus*. Also, these sharks, *Parmaturus*, have comparatively short snouts and broad heads, much different in general shape from members of the genus *Galeus*. One other cat shark, *Apristurus profundorum* (Goode and Bean), also has denticles on the upper margin of the dorsal fin differing in size and shape as well as in spacing from denticles on the lateral surfaces of the tail and most other parts of the body (see fig. 23). The crest is less well defined in *Parmaturus* than in *Galeus*, and in *Apristurus profundorum* there are no enlarged and projecting denticles marking the margin of a crest.

The presence of an upper caudal crest with

much enlarged marginal scales, the crest not extending appreciably onto the lateral surface of the tail, appears to be a unique feature of *Galeus* and sufficient for diagnosis in the present treatment of scyliorhinid genera. Other characters, such as the long and structurally specialized claspers, may also be useful in the definition of the genus; but until more Pacific and eastern Atlantic specimens have been examined, I wish to avoid tampering with generic definitions and will rely on characters clearly outlined in the literature.

Species of the genus as presently understood may be divided into two groups on the basis of color pattern. One group comprises plain colored species, sometimes with fin markings of contrasting color but without a pattern of cloudy spots or blotches generally distributed over dorsolateral surfaces. Plain colored species are *Galeus sauteri* (Jordan and Richardson) of the western Pacific and *Galeus jenseni* (Saemundsson) and *Galeus murinus* (Collett) of the northeastern Atlantic. Another western Pacific species, *Galeus hertwigi* (Engelhardt), said to have a short snout and a tail with contrasting color pattern, has been included in the genus *Galeus* by Fowler (1941).

The other group of the genus is characterized by the presence of a pattern of blotches or spots over the dorsolateral surfaces. This group includes *Galeus melastomus* Rafinesque of the eastern North Atlantic, *Galeus polli* Cadenat from the west coast of Africa, and the western Atlantic forms treated here. In addition, a Pacific species, *Galeus eastmani* (Jordan and Snyder, 1904), has been described as having "indistinct clouds of deeper shade." It appears from examination of the type (SU 7740) that these markings are less pronounced than in any of the western Atlantic forms. *Galeus eastmani* differs markedly from Atlantic species in being more slender, having a more sharply pointed snout, having a larger spiracle, and in having heavier denticles.

KEY TO ADULT SPECIMENS OF WESTERN ATLANTIC *GALEUS*

1A. Anal fin long, its origin under a vertical through the posterior tip of the first dorsal fin and its rear tip nearly reaching (to within one-half diameter of the eye) origin of lower caudal lobe.. *Galeus cadenati* n. sp.

1B. Anal fin short, its origin in back of a vertical through the posterior tip of the first dorsal fin and its rear tip separated from the origin of the lower caudal lobe by a distance equal to the horizontal diameter of the eye or more..... *Galeus arae* (Nichols)

Galeus arae (Nichols), 1927

Figures 4, 5, 7, 20, 21, and 27; tables 1, 5, and 6.

Galeus arae is a much smaller species than *G. melastomus* of the eastern North Atlantic and Mediterranean. None of the *G. arae* seen exceed 37 cm. while *G. melastomus* reaches a length of over 90 cm. *G. melastomus* lays eggs in leathery cases similar in general appearance to egg cases of other scyliorhinids. Although adult female *G. arae* with large ovarian eggs have been collected, none have been observed with eggs or embryos in the oviducts and no egg cases have been collected that can be referred with confidence to western Atlantic *Galeus*.

Galeus arae is very commonly taken in shrimp trawls off the coast of Florida, both in the Atlantic and the Gulf of Mexico. Examples have been recorded for more than 100 stations of exploratory fishing vessels, usually with several specimens from each station. Collections from single hauls indicate strong tendencies to segregation by size and sex, but no well-defined pattern in the depth of occurrence of immature or of adult males or females has appeared.

The records at hand show *Galeus arae* to be locally common from about 330- to 460-m. depth around Florida, from the offings of Jacksonville to Pensacola, and usually at greater depths, 400 to 620 m., in the Yucatan Channel, near Pedro Bank and Jamaica, and around some of the banks and islands of the Caribbean off the coasts of Nicaragua and Costa Rica southward to lat. 13°30′ N. Three atypical specimens from the vicinity of Puerto Rico, provisionally referred to *G. arae*, are from 293- and 402-m. depth. The Puerto Rican specimens are more robust than the typical *G. arae* and have a poorly defined pattern of spots (fig. 20C). They may represent an undescribed species, but closely resemble *G. arae* in morphology and proportions. Larger series are needed to assess the status of the Puerto Rican specimens.

Bigelow and Schroeder (1948), referring to a series of specimens taken off Tortugas and off the north coast of Cuba, note that one specimen of about 295 mm. has claspers falling short of the tip of the pelvics, while in another male of 317 mm., the claspers extend far beyond the tips of the

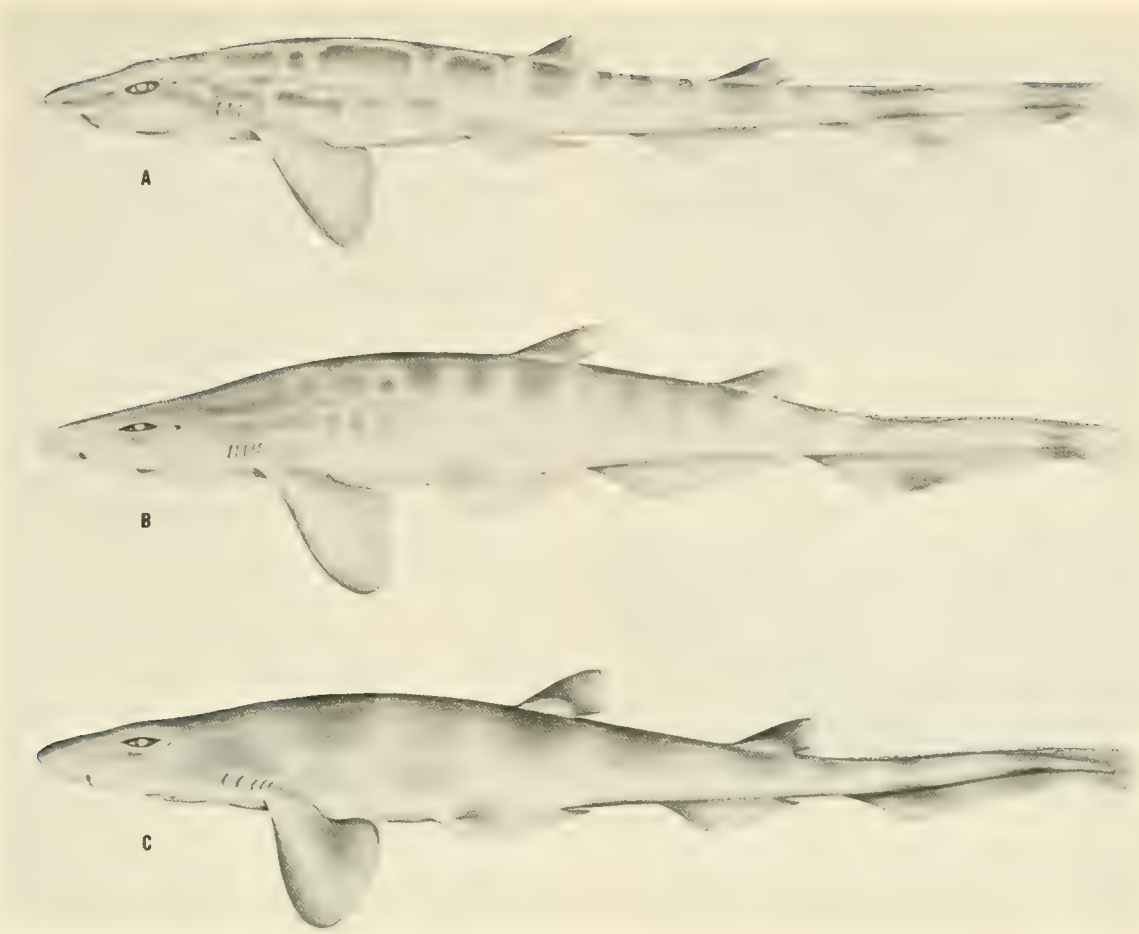

FIGURE 20.—A, *Galeus arae* (Nichols), drawn from a 290-mm. female; B, *Galeus cadenati* new species, drawn from a 300-mm. female; C, *Galeus arae*, drawn from a 320-mm. female from Puerto Rico, showing color pattern found on large examples from that area.

pelvics. From this they conclude that maturity is probably attained at about 300 mm. The extensive series of *G. arae* that I have examined includes large numbers of adult males from the Florida and Central American slope. These are 265- to 290-mm. specimens for the most part, and no examples of either sex exceed 330 mm. The specimens from Puerto Rico already mentioned include two adults, a 368-mm. male, and a 352-mm. female. They are not only appreciably larger than any observed from the continental slope but also differ in some body and fin proportions. As shown in table 6, the Puerto Rican specimens have a proportionally shorter anal fin and differ in other measurements from Florida examples of *G. arae*.

Galeus cadenati new species

Figures 20, 21, and 27; tables 1, 5, and 6.

Holotype.—A female 303 mm. in total length, USNM 260468, F1 collected at R/V *Oregon* station 3592, lat. 09°13′ N., long. 80°44′ W., in 439-m. depth off the Caribbean coast of Panama, May 30, 1962.

Diagnosis.—A small species of the genus *Galeus* differing from *G. arae* in having a comparatively longer anal fin (13.2 to 15.0 percent of total length compared to 8.7 to 13.6 percent in *G. arae*) with the tip of the anal reaching nearly to the lower caudal origin, separated from it only by a distance less than half the horizontal diameter of the eye as compared to separation by a distance equal to the horizontal diameter of the eye or more in *G. arae*. The pectoral fins and the two dorsal fins of

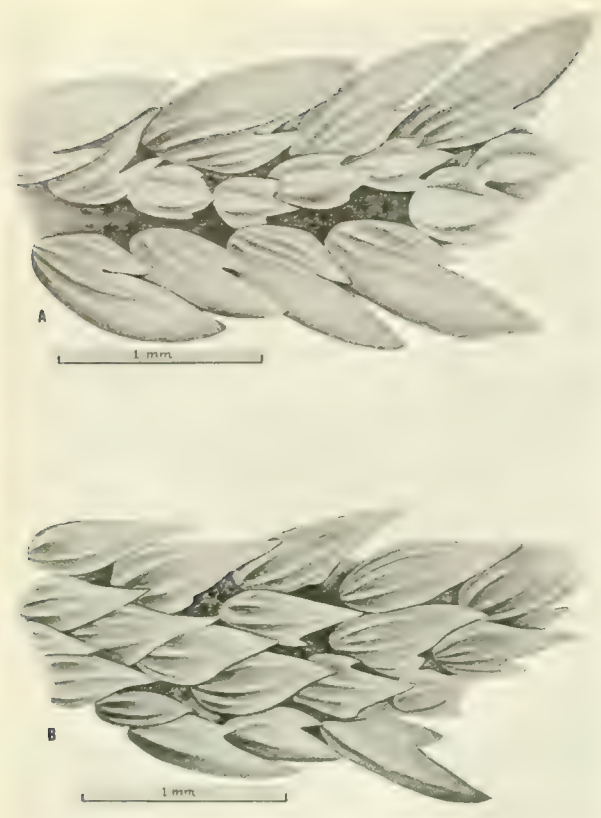

FIGURE 21.—Enlarged scales of caudal crests drawn from sections near the origin of upper caudal lobes of: A, *Galeus arae;* and B, *Galeus cadenati.*

G. cadenati are proportionally somewhat longer than the fins of *G. arae* (table 6). Minor differences in the caudal crest are shown in figure 21, the crest in *G. cadenati* being about three-fourths the width of the crests in *G. arae* of comparable size.

This species is similar to *Galeus polli* Cadenat, 1959, which is found abundantly on the west coast of Africa. I have compared specimens of the new species with a large series of *G. polli*, including examples from several localities, collected by vessels of the Guinean Trawling Survey and loaned to me through the Smithsonian Institution Sorting Center. Both *G. polli* and *G. cadenati* have long anal fins and are readily separable from *G. arae* on this basis. *G. polli* has a longer snout (as measured from the front of the mouth) and a narrower head than *G. cadenati*, but proportional differences in snout length and distance between the nostrils are not great in all specimens at hand. In Cadenat's table (1959) of proportions for four large adult *G. polli*, distances from the top of the snout to the front of the mouth are shown as 7.4 to 8.5 percent of total length as compared to 6.0 to 7.3 percent in our specimens of *G. cadenati.*

Differences between *G. polli* and *G. cadenati* that are not especially notable in comparison of measurements are easily seen in side by side comparison of the two species. *G. cadenati* has a more robust form, a wider and shorter head, and a wider and shorter mouth. The color differences in the specimens examined are also striking. The specimens of *G. cadenati* are brown with the spots and saddles of the posterior part of the trunk rather indistinct. All of the specimens of *G. polli* available for examination are grayish with black or nearly black spots and saddles. In most of the specimens the spots and saddles are more clearly defined; but a few specimens are dark all over, and the spots and saddles are indistinct.

Description of the holotype.—Measurements of the type, USNM 260468-F1, are given in table 5, and the color pattern in the type does not differ appreciably from that illustrated (fig. 20B) for the species. Body moderately slender, caudal axis not elevated, body sector (tip snout to anus) about two-fifths of total length; head broad, snout moderately pointed and not greatly flattened dorsoventrally, with large, medially located, and elongate patches of mucous pores above and below, the pore openings small, arranged in irregular rows; nasal apertures large, about half the length of snout measured to front of mouth, oblique, with a triangular flap covering the posterior opening when closed, well separated from mouth; mouth large with labial grooves above and below, the lower longer, reaching about one-fourth the distance toward the symphysis; eye large, oval, length of orbit more than two times its width, no functional nictitating membrane, but a subocular fold; spiracle moderate, located immediately behind and slightly below level of horizontal axis of eye; gill openings short, longest about half the horizontal diameter of eye, the fourth and fifth located above the origin of the pectoral; pectoral long, about two times length of snout and broad, its greatest width about two-thirds the length of its anterior margin, its distal corners rounded; first dorsal fin origin nearly over middle of pelvic base, its distal margin only slightly convex, its apical and lower tips moderately rounded; second dorsal fin about

as large as first dorsal; dorsal fin bases separated by a distance about equal to length of anal base; second dorsal similar in shape to first dorsal, its origin posterior to middle of base of anal, its posterior tip separated from origin of caudal crest by a distance equal to one-half horizontal diameter of orbit; pelvic fins large and long, united and adnate to body for a short distance posterior to anus, their posterior tips pointed; anal fin long, its base 2½ times base of first dorsal, its height about equal to height of second dorsal; upper caudal with crest of modified denticles (see fig. 21B), caudal fin slightly less than one-third total length; lower caudal fin about same height as anal, its margin rounded without forming a pointed lobe, a notch near the tip.

Denticles over dorsolateral surfaces small, three pointed, the central point much the longest, similar to denticles of *G. arae* (see fig. 7).

Teeth relatively small, multicusped, largest three or five cusped with central cusp much the longest, similar in shape in upper and lower jaws, several series functional; upper teeth in 31+31 rows; lower teeth in oblique series, not readily counted by row.

Notes.—Galeus cadenati, so far as known, is found only in the southwestern Caribbean off the coast of Panama. Although this is quite near the range of *Galeus arae*, which occurs off the coast of Nicaragua, the collections seen show no overlapping.

Eastward and along the Caribbean or Atlantic coasts of Columbia, Venezuela, the Guianas, and northern Brazil, specimens of *Galeus* have not been reported although collections from these areas have produced many small sharks of other genera in depths at which *Galeus* would be expected to occur.

Genus *Apristurus* Garman, 1913

Type species *Scylliorhinus indicus* Brauer, 1906, by original designation.

The genus *Apristurus* as understood here (*Pentanchus profundicollis* Smith and Radcliffe is excluded) contains about 16 species. Four western Atlantic species are recognized. Members of the genus are small sharks, for the most part less than a meter long, with broad and flattened heads which are sometimes described as shovel-shaped. All of the known species are rather uniform black or dark brown in life. Lighter colors on some museum specimens (*Apristurus profundorum*) are thought to be due to handling accidents or to effects of preservatives.

Various sets of characters have been used in descriptions of species of *Apristurus*, but most authors have relied on morphometrics to define species. This has not been very satisfactory because some descriptions have had to rest on single specimens and at best the series are small. Added to this, specimens of *Apristurus* preserved in alcohol quickly become wrinkled and fragile. Measurements are difficult to make, and the body proportions and fin positions in the series measured appear to vary considerably within species.

So far as known, all species inhabit deep water, specimens for the most part being taken from depths of more than 600 m.

KEY TO WESTERN ATLANTIC *APRISTURUS*

1A. Denticles over most dorsolateral areas narrow, erect, not imbricate, their bases separated by distances greater than the diameter of a denticle base; a caudal crest of wide, imbricate denticles of about uniform size, their tips not pointed upward, forming a rather smooth surface, extending a short distance onto the lateral surface of the tail, the crest denticles in sharp contrast (see fig. 23) to the very sparsely scattered, narrow and erect denticles of the lateral surface of the tail; pelvic fins comparatively short, somewhat thickened, broadly ovate in shape; anal fin relatively high, its anterior and distal margins forming a continuous smooth curve ---------- *Apristurus profundorum*

1B. Denticles over most dorsolateral surfaces moderately broad, close together, imbricate or at least very closely arranged with small spaces between bases; denticles of upper margin of tail not differing greatly in shape, size or density of arrangement from denticles of lateral surfaces of tail; pelvic fins comparatively long, lanceolate; anal fin either high or low but with its anterior margin and distal margin forming an angle, the two margins not rounded as a continuous curve---------- 2A or 2B

2A. Head comparatively narrow with narrow band of prominent mucous pores of underside of snout extending medially from front of mouth nearly to tip of snout in four or sometimes six longitudinal rows; tip of snout notably constricted at anterior end of nostrils; teeth comparatively large and sexually dimorphic ---------- *Apristurus riveri*

2B. Head comparatively broad with a wide band of prominent mucous pores of underside of snout extending medially from front of mouth nearly to tip of snout in eight or more longitudinal rows; tip of snout not notably narrowed at nostrils; teeth comparatively small with no sexual dimorphism--------- 3A or 3B

3A. Second dorsal fin substantially greater in area than first dorsal fin; first dorsal fin origin usually behind posterior end of base of pelvic fins ---------- *Apristurus indicus*

3B. First and second dorsal fins of nearly equal area; first dorsal fin origin over the middle of the pelvic base ---------- *Apristurus laurussoni*

***Apristurus profundorum* (Goode and Bean), 1896**

Figures 7, 22, 23, 25, and 27; tables 1, 7, and 8.

The type specimen of *A. profundorum*, USNM 35646, is in quite poor condition and very fragile. The fins are frayed, the skin looks scuffed, and the general impression given is that denticles, pieces of skin, and pieces of fins must be missing. Actually very little is missing although there is no doubt that the specimen had been severely damaged either when captured or during 69 years of its existence as a preserved specimen. Some questions about this specimen came up during the course of preparation of a report on sharks (Bigelow, Schroeder, and Springer, 1953), and if my memory is correct it fell to my lot to reexamine it. Apparently my reexamination missed some of the important features, and I am thus primarily responsible for failure to note that the material studied and held to be *profundorum* in that report included two species.

A. profundorum is easily separated from the other three western Atlantic species by the characters given in the preceding key. Several differences also are evident from table 8 which shows ranges of measurements in the series examined. These ranges of measurements show a lesser distance from the tip of the snout to the origin of the first dorsal fin than in the other three western Atlantic species and a lesser distance from the tip of the snout to the origin of the second dorsal. The table also shows a wide degree of variation in proportions for all *Apristurus*.

The teeth of the type, an adult male, are in 25+25/25+25 rows, and the teeth of a smaller female specimen, MCZ 38299, are in 31+31/25+25 rows. The teeth are difficult to count because they are arranged in alternate series, and the number of functional series varies from about five near the symphysis to three or less at the corners of the jaw.

The type of *profundorum* was collected from 1,492 m. off Delaware Bay, and the specimens included in the series of five specimens measured here was collected by the M/V *Cap'n Bill II* at depths from 686 to 1,317 m. off New Jersey and New England.

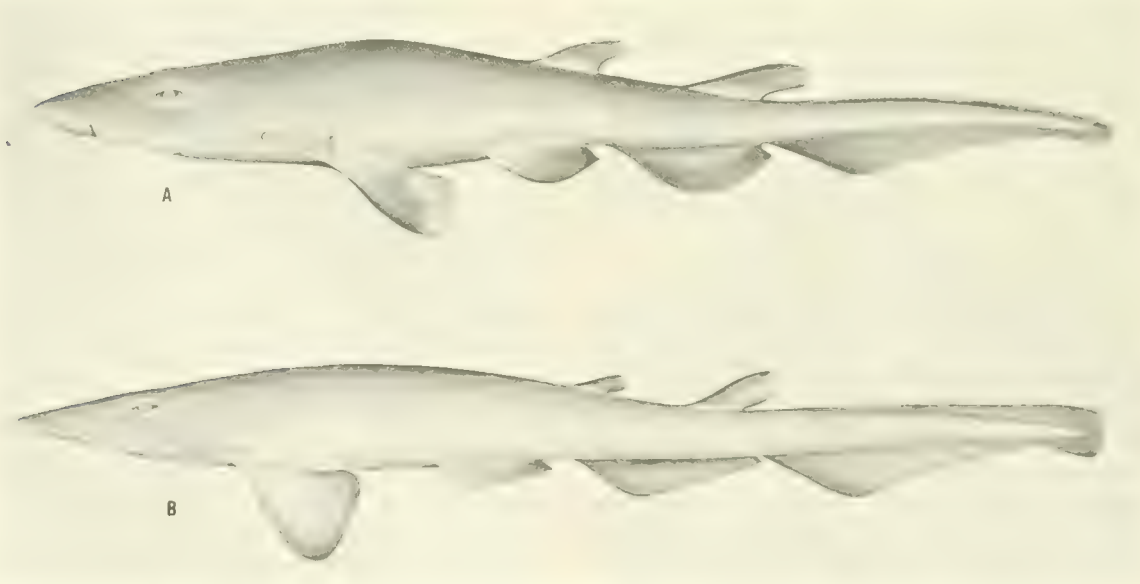

FIGURE 22.—A, *Apristurus profundorum* (Goode and Bean), drawn from a 390-mm. female, MCZ 38299; B, *Apristurus indicus* (Brauer), drawn from a 395-mm. female from M/V *Oregon* station 3586.

FIGURE 23.—Lateral view of portion of caudal fin of *Apristurus profundorum* (Goode and Bean), showing closely packed denticles on and near the upper margin of the fin and the widely spaced denticles on the lateral surfaces of the tail.

***Apristurus indicus* (Brauer), 1906**

Figures 9, 22, and 27; tables 1, 7, and 8.

It is clear that the western Atlantic specimens of *Apristurus* at hand may be divided into four groups on the basis of characters given in the preceding key. Three of these groups of specimens clearly represent respectively *Apristurus profundorum* (Goode and Bean), *A. riveri* Bigelow and Schroeder, and *A. laurussoni* (Saemundsson). The fourth group includes specimens referred to *Apristurus atlanticus* (Koefoed) by Bigelow and Schroeder (1948) and Bigelow, Schroeder, and Springer (1953). The specimens available for examination are about 40 examples from the Gulf of Mexico, the Caribbean, and adjacent Atlantic waters, most of them immature. All are referred to *Apristurus indicus* (Brauer) with some missgiving because *A. indicus* has been regarded as restricted to the Indian Ocean.

Koefoed states (1927) that *atlanticus* is related both to *profundorum* Goode and Bean, and *indicus* Brauer, but that it differs in having a larger eye. From Koefoed's measurements of the type, a 247-mm. specimen from the Atlantic near Gibraltar, it can be calculated that the orbit is 4.9 percent of the total length. Among the specimens referred here to *A. indicus*, the orbit is 2.5 to 4.0 percent of the total length and in available specimens of other Atlantic species 2.2 to 3.9. Koefoed's figure of the type of *atlanticus* (1927, pl. 3, fig. 3) shows the second dorsal fin only slightly larger in area than the first. In Western Atlantic specimens of *A. indicus* the second dorsal fin has less than half the area of the first dorsal. Furthermore, Koefoed specifically states that the first and second dorsal fins of *atlanticus* are equally large.

The number of tooth rows in the western North Atlantic specimens of *A. indicus* at hand varies from 33+33/33+33 to 45+45/45+45. The teeth of these specimens are much smaller and more numerous than in *A. profundorum* and *A. riveri*. Although the teeth of *A. laurussoni* are slightly larger than in the *A. indicus* specimens, the difference is not great enough to be notable except on direct comparison of specimens of equal size.

***Apristurus riveri* Bigelow and Schroeder, 1944**

Figures 4, 5, 7, 10, 11, 24, and 27; tables 1, 7, and 8.

In one haul with a 40-foot shrimp trawl at M/V *Oregon* station 3586 off the Caribbean coast of Panama, five *Apristurus* of about equal size were taken. The haul was made in 860 to 914 m. A temperature determination at the bottom was not made at this station but in nearby stations the following temperatures were recorded: 366 m., 11.6° C; 457 m., 8.8° C; 750 to 768 m., 5° C. Four of the specimens collected were adults of *A. riveri*, one male and three females. The fifth specimen was an immature example of *A. indicus*. Of the three female *riveri*, one had short filamentous processes of egg cases protruding. In all three the cloacal area was surrounded by a flattened ring of white tissue. All had large eggs (10–12 mm. diameter) in the single ovary, and one had egg cases with eggs in both oviducts. The egg cases were about 50 mm. long, not including filaments, and about 15 mm. in greatest width. The shells appeared to be smooth surfaced. The egg shells were not completely formed or finished at their inner ends, and the nature of the processes at the posterior ends could not be determined, except that they were not the single tendrils at each corner found in *Scyliorhinus* but were more numerous and arranged as a filamentous fringe across the end of the case. The cases were greenish, semitransparent, and with some longitudinal lines of lighter color.

The uniformly flattened cloacal area was apparent as an unusual feature of the specimens only when they were fresh or were preserved in formalin. After transfer to alcohol this flattening disappeared.

The presence of an adult male in the haul also revealed the remarkable difference in tooth size and shape (fig. 10) between adult males and females. Although later collections produced another adult male from near Key West, the only immature specimens seen thus far have been females, so it has not been determined when the tooth dimorphism first appears.

The teeth in the six specimens examined are in 24+0+24/19+0+19 to 29+0+29/22+0+21 rows with no teeth at the symphysis in either jaw. The teeth of the females are generally tricuspid in the central portion of the jaws but have five, seven, or nine cusps toward the angles of the jaws. The number and shape of the teeth of females of the series described here are about as described for *A. riveri by* Bigelow and Schroeder (1944, 1948). Using the definition of series of teeth given earlier in this paper, however, the number of functional series in *riveri* is five or six. The tooth arrangement, as in other *Apristurus* or, for that matter, in all scyliorhinids, is in alternate series with series defined as teeth arranged along a single line parallel with the axis of the jaw. This arrangement gives the appearance of diagonal rows (see fig. 11). It may be described also as Bigelow and Schroeder (1944) have done as an arrangement in quincunx.

In dealing with somewhat larger series than were available to Bigelow and Schroeder, some difficulties have appeared in the use of distances between gill openings and angles formed by the labial grooves as means for differentiating species, because of greater variation in the larger series. Among western Atlantic species the narrower head of *riveri* seems the most outstanding and reliable criterion for quick identification. The comparatively narrower head is shown quite clearly in figure 27. In *riveri* the band of pores on the underside of the snout is consistently narrower than in other western Atlantic species, generally being composed of about four rows of pores instead of eight or more.

The claspers of the adult males are rather short, reaching about 2.3 percent of total length beyond the tips of the pelvic fins, and quite stout. There are no hooks. The clasper siphons are also relatively short, extending only about 10 mm. in advance of the origin of the pelvics.

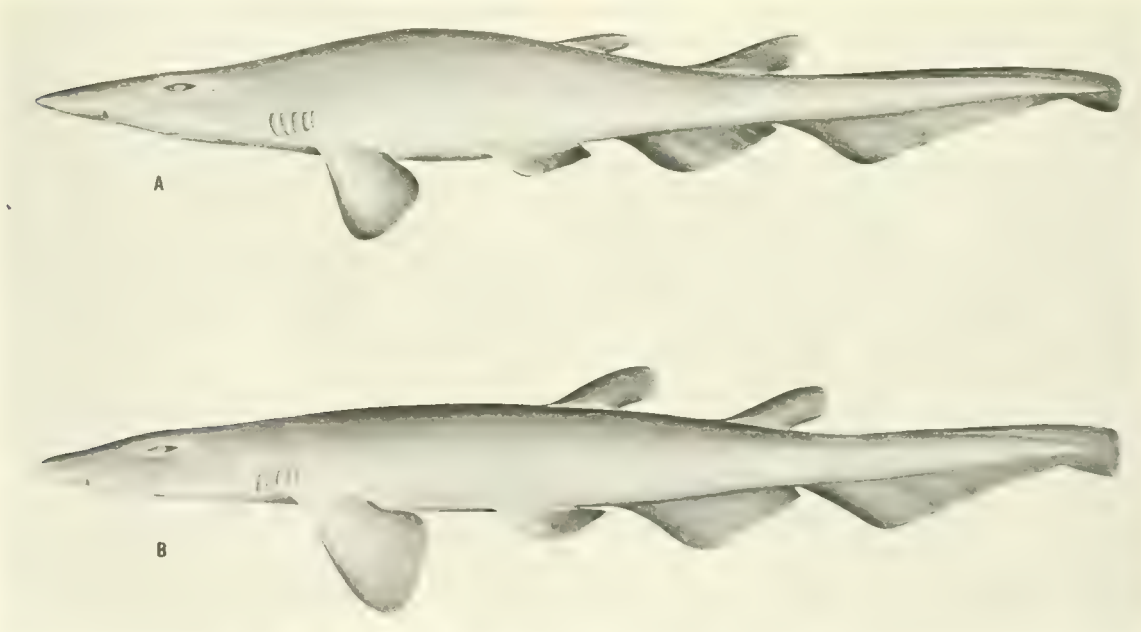

FIGURE 24.—A, *Apristurus riveri* Bigelow and Schroeder, drawn from a 400-mm. female from M/V *Oregon* station 3586; B, *Apristurus laurussoni* (Saemundsson), drawn from a 540-mm. male, MCZ 38406.

Apristurus laurussoni (Saemundsson), 1922

Figures 24, 25, and 27; tables 1, 7, and 8.

Saemundsson's only specimen, the type of *Scyllium laurussonii*, was a 673-mm. female. This specimen, which is in excellent condition, was examined through the courtesy of the Natural History Museum, Reykjavik, as a loan. It differs from the type specimen Goode and Bean of *Scylliorhinus profundorum* 1896, with respect to characters given in the preceding key.

The separation of the broadheaded *A. laurussoni* from the narrow-headed *A. riveri* and the separation of *A. laurussoni* from *A. profundorum* on the basis of the pelvic shape (see fig. 25) or the denticle distribution problem presents no difficulty except perhaps in very small specimens.

FIGURE 25.—Diagram to show shapes of pelvci fins: At left, *Apristurus profundorum;* at right, *Apristurus laurussoni.*

A. laurussoni differs from our specimens of *A. indicus* in having the two dorsal fins of approximately equal size. In A. indicus the first dorsal fin has about half the area of the second. Both *laurussoni* and *indicus* in the material examined are quite variable in number of tooth rows, number of vertebrae, and fin positions.

The teeth of *A. laurussoni* are small and comparatively numerous in 34+0+34/34+0+32 to 42+0+41/53+0+43 rows. The two largest males examined, 520 and 540 mm., are apparently immature, but there is no indication of sexual dimorphism in teeth in comparison with a 580-mm. female or the type, a 673-mm. female. Saemundsson (1922) noted that the teeth of the type are in 22 rows on each side of the symphysis. My count of the teeth of the type specimen is approximately 41 rows on each side. This difference is the result of a different method of counting rows. The alternate arrangement of teeth together with their generally small size makes routine tooth counting in *Apristurus* impractical. In many specimens the diagonal rows are very prominent and seem to be the logical ones to count. In our specimens if diagonal rows were counted, the tooth formula would be close to that given by Saemundsson.

It may be helpful to subsequent workers with the genus to note that Goode and Bean's type and only specimen of *profoundorum* is an adult male while their illustration (1896, pl. 5, fig. 16) appears to be a female. Saemundsson's text references to illustrations on plate V (1922, pp. 173 and 200) for *Pristiurus Jensenii* and *Scyllium Laurussonii* are reversed, and the illustration of the lateral view of a shark in Bigelow and Schroeder (1948, fig. 38) captioned as the type of *profundorum* may not represent that species since the illustration shows either a female or a male with claspers not showing, while the type is a male with claspers extending past the tips of the pelvics.

Exclusive of the type which was collected from 560-m. depth near Vestmanneyjar, off the southern coast of Iceland, I have examined about 25 specimens that I refer to the species. These are from the northern half of the Gulf of Mexico and from the Atlantic coast of the United States from latitude 40°40′ N. (off Massachusetts) southward to 38°41′ N. (off Delaware). Specimens were taken from depths of 760 to 1,460 meters.

Genus *Halaelurus* Gill, 1861

Type species—*Scyllium bürgeri* Müller and Henle, 1841, by original designation.

The group of scyliorhinid sharks usually assembled in the genus *Halaelurus* seems to include leftovers and poorly known species. It is in special need of nomenclatural revision. Changes can best be made in a general revision of the world's scyliorhinid genera, which will require more extensive collections than are available now.

The American representatives of *Halaelurus* have long and strong labial grooves along both upper and lower jaws and thus differ from American species of the genus *Scyliorhinus* which have weak and short labial folds only on the lower jaw. The

two South American species considered here both have patterns of dorsal saddles somewhat resembling those in *Scyliorhinus* and from this feature can be readily separated from *Apristurus*. They have no caudal crests and so differ from *Galeus*. They differ from *Schroederichthys* in having caudal trunk sections somewhat shorter, in having much longer and more prominent labial folds, and

FIGURE 26.—A, *Halaelurus chilensis* (Müller and Henle), an immature male collected at Coquimbo Bay, at lat. 29°56′ S., on the coast of Chile (the pelvic fin of this specimen has been damaged); B, *Halaelurus bivius* (Guichenot), collected near Puerto Montt, Chile, at lat. 41°54′ S.

in having a reduction (in the larger specimens examined) in the number and size of the accessory cusps on the teeth of the lower jaw.

In many features the *Halaelurus* of the southern part of South America resembles *Schroederichthys*. Dr. Elvira Siccardi who has examined many specimens from Argentina has called my attention (in personal communication) to several

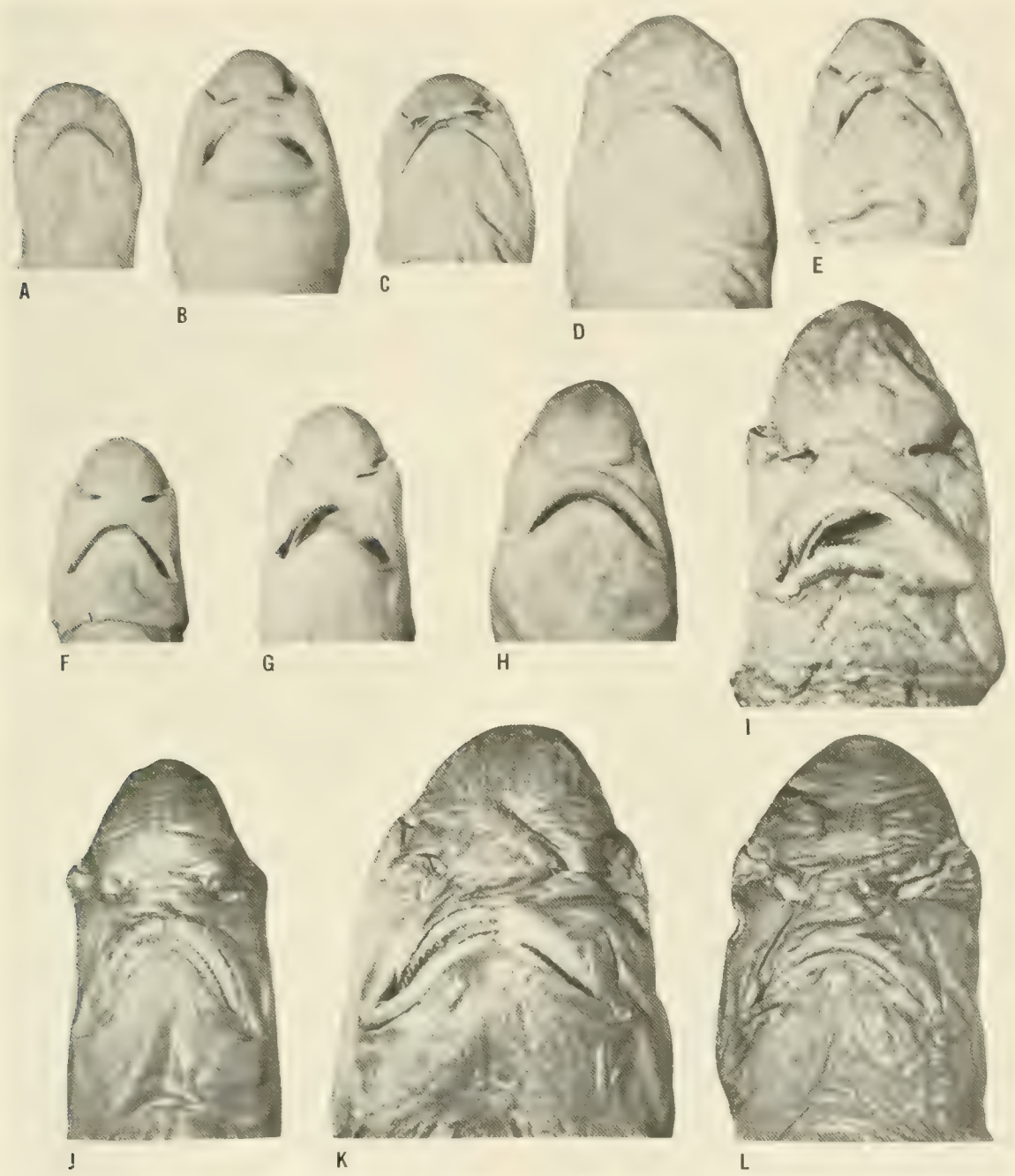

FIGURE 27.—Photographs of lower side of heads: A, *Scyliorhinus torrei;* B, *Scyliorhinus retifer;* C, *Scyliorhinus meadi;* D, *Scyliorhinus hesperius;* E, *Scyliorhinus boa;* F, *Galeus arae;* G, *Galeus cadenati;* H, *Galeus arae;* I, *Apristurus profundorum;* J, *Apristurus riveri;* K, *Apristurus laurussoni;* L, *Apristurus indicus.*

similarities such as the development of long, very slender nasal flaps in species of each genus (*H. bivius* and *S. tenuis*), the relatively short caudal lobes in combination with long postpelvic trunk in both groups, and certain somewhat subtle similarities in denticle structure.

Problems in connection with names to be applied to South American *Halaelurus* cannot be adequately treated here because of insufficient study material. My view that more species than *Halaelurus chilensis* (Guichenot, 1847) and *Halaelurus bivius* (Müller and and Henle, 1841) are involved in the material described by various authors has been strengthened by discussions with Dr. Siccardi.

Some unresolved questions on the status of types add to the difficulties with nomenclature. The types of both *H. bivius* and *H. chilensis* are stuffed specimens. The specimen designated as the type of *bivius* by Günther (1870) is said to be from southwest Africa but Günther's description is not in close agreement with the earlier description of Müller and Henle (1841). The confusing synonomy of *bivius* can be seen in the treatment given in Norman's work (1937) on Patagonian fishes.

It seems probable that all of the accounts of South American *Halaelurus*, including this one, have been based on material quite inadequate to delineate species. Available material suggests that considerable differences in some characters may exist between young and adults of the same species. This makes the development of meaningful synonymy impractical. It is possible that both Berg (1895) and Lahille (1921, 1928) discussed the form here referred to *H. chilensis* under the name *bivium* or *bivius*. Vaillant's account (1891), under *Scyllium chilense* Guichenot, states that he believes *Scyllium bivium* Smith is not a distinct species, but goes on to state that all the small examples he had seen were females.

A more extensive study of these scyliorhinids should provide some answers of great interest to the phylogeny of carcharhinid sharks because these sharks, perhaps considered together with *Schroederichthys*, have more characters approaching the carcharhinid line than do other scyliorhinids. The longer jaw of *H. bivius* together with lower jaw spikelike teeth is a feature more familiar in the Carcharhinidae than in the Scyliorhinidae. The claspers and clasper siphons of *Schroederichthys* bear many resemblances to those of the carcharhinids.

Halaelurus bivius (Müller and Henle), 1841

Figure 26; tables 7 and 8.

The specimens of *H. bivius* from Chile examined for this report are very easily separated from Chilean examples of *H. chilensis* by differences in general shape. As can be seen in the photographs (fig. 26), *H. chilensis* has a shorter head, a somewhat shorter and definitely less pointed snout, and a shorter and much less strongly arched jaw.

The specimens of *H. chilensis* examined were immature, showing a well-marked series of enlarged denticles in rows along the back, and in this differed from the adult *H. bivius* available for comparison. The specimens of *H. bivius*, however, had some enlarged dorsolateral denticles.

In direct comparison of *H. bivius* with *H. chilensis* specimens, it was noted that the nasal flaps of *H. bivius* were longer and narrower, the gill slits were somewhat longer, the anal fin base was somewhat longer (see table 7 and 8), and the denticles prevalent on dorsolateral surfaces had longer points.

Halaelurus chilensis (Guichenot), 1847

Figure 26; tables 7 and 8.

Based on specimens from the Pacific coast of South America, it appears that there are relatively great differences between *H. chilensis* and *H. bivius*. It should be noted, however, that all of the specimens of *H. bivius* seen were adult males while all the specimens referred to *H. chilensis* were immature.

SUMMARY AND COMMENT

To have accomplished its purpose, this study should have indicated some of the kinds of information about catsharks needed for an adequate revision of the family. Great variation within species, particularly in morphometrics, the occurrence of sexual dimorphism (at least in one species), and the finding of a new genus and several new species point to the need for more comprehensive collections from the continental slopes and from ocean basins as a basis for understanding the group.

Western Atlantic scyliorhinids all have been taken at depths where relatively cool temperatures prevail; and in the course of a more general study of the group, it will be interesting to note which,

if any, species enter relatively warmer areas or shallow-water areas. The discovery by Poll (1951) and Cadenat (1959) that the ovoviviparous condition and the oviparous condition both occur within a single genus (*Galeus*) points to the need for much more observation on life histories of catsharks.

The order in which genera are taken up in this paper is not intended to have any phylogenetic implication. *Galeus*, *Apristurus*, and *Schroederichthys*, as far as these are known at present, are quite compact groups of similar species and are separable from each other and from other of the world's scyliorhinid genera by many differences.

The separation of *Scyliorhinus* from *Halaelurus* and from some other genera of the Indo-Pacific region has, in the past, been based primarily upon differences in the arrangement of skin folds near the mouth, by the presence or absence of nasoral grooves, and by the relative development of anterior and posterior nasal valves. Keys to genera and also to species used by Garman (1913) and by Fowler (1941) emphasize these characters. I have given little descriptive space to them because they appear to be of little use for determination of western Atlantic species and also because they are somewhat variable in the specimens at hand. I have also had some difficulty in understanding the terminology. For example, Garman (1913) states that nasal cirri are absent or rudimentary in *Scyliorhinus*, but he separates *Poroderma*, an Indian Ocean genus, from *Scyliorhinus* in his key by the complete absence in *Poroderma* of a rudimentary nasal cirrus. This rudimentary cirrus, in the material I have examined, is merely a thickening of a portion of the anterior nasal flap, broader and thicker near the base of the flap, narrower and thinner near the posterior margin of the flap, but not extending at all beyond the edge of the flap. If one is familiar with the shape of nasal cirri of orectolobid sharks, this structure looks like a nasal cirrus entirely embedded in the flap. I find it difficult to accept the idea that this is necessarily a rudimentary structure and suspect that it may function in directing the flow of water past the nasal aperture.

Nevertheless, differences in skin structures near the mouth and nasal apertures may be of great usefulness in the practical description of species and as criteria for their identification, especially among Indo-Pacific forms.

TABLE 3.—*Measurements of selected examples and type specimens of Atlantic* Scyliorhinus

Species	*S. retifer*	*S. meadi* (type)	*S. hesperius* (type)	*S. boa*	*S. torrei*	*S. caniculus*	*S. stellaris*
Museum No. or Station No.	ORE 4153	USNM 188049	USNM 187732	USNM 186195	SB 2457	USNM 195851	USNM 34352
	Mm.	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*
Total length	465	247	415	346	270	383	370
Tip of snout to—							
Anterior nasal aperture	12	8	11	10	6	7	9
Posterior nasal aperture	19	11	18	15	8	14	13
Front mouth	21	12	21	17	10	14	14
Eye	21	13	24	21	11	16	15
Gill I	74	36	69	50	35	46	52
Gill V	97	45	87	69	48	62	71
Origin pectoral	85	40	82	65	45	59	64
First dorsal fin	237	116	210	180	140	182	185
Pelvic fins	194	107	176	145	105	148	160
Anal fin	282	143	252	213	162	213	220
Second dorsal fin	314	153	283	238	188	251	242
Lower caudal fin	346	180	315	268	210	292	275
Upper caudal fin	354	185	320	274	215	298	285
Anus	203	112	190	155	114	156	170
Length upper caudal fin	108	63	95	72	55	85	85
Base first dorsal fin	28	15	26	23	18	25	26
Base second dorsal fin	24	13	21	17	12	20	24
Base anal fin	34	22	38	25	22	37	36
Distance between dorsal fins	52	26	44	37	33	46	32
Internasal distance	7	15	7	7	5		5
Length orbit	20	9	15	13	9	11	13
Length lower labial fold	9	5	7	3	5	12	8
Length upper labial fold							
Width mouth	34	20	34	25	19	22	25
Length mouth	20	11	14	15	10	9	16
Height gill I	9	6	7	6	5	9	6
Height gill V	4	4	4	4	2	4	3
Tip second dorsal to caudal	9	13	9	7	10	20	13
Tip pelvic to second dorsal	71	25	59	48	49	59	40
Tip pelvic to anal	44	13	33	31	25	21	22
Tip pelvic to lower caudal	106	55	95	86	76	100	77
Length outer margin pectoral	70	33	62	45	26	46	44
Length anterior margin first dorsal	45	25	41	32	22	33	39
Length anterior margin second dorsal	34	19	31	25	13	27	34
Length anterior margin anal	30	21	33	24	20	27	29
Distance eye to spiracle	3	3	3	3	2	3	4

TABLE 4.—*Range of total lengths and range of measurements expressed as percent of total length in western Atlantic* Scyliorhinus

Species	*S. retifer*	*S. meadi*	*S. hesperius*	*S. boa*	*S. torrei*
Number of specimens measured	10	5	13	7	7
Length range in millimeters	173–465	183–264	160–466	143–346	129–270
Tip of snout to—	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*
Anterior nasal aperture	2.3–3.4	3.0–3.8	2.3–4.0	2.5–3.5	1.4–2.2
Posterior nasal aperture	3.6–4.7	4.2–4.5	3.7–5.1	3.8–4.9	2.7–3.9
Front mouth	4.4–5.8	4.4–4.9	4.5–5.7	4.2–5.6	3.5–4.7
Eye	4.5–6.1	5.3–6.0	5.0–6.8	5.2–6.3	4.1–5.4
Gill I	14.1–16.5	13.1–15.8	14.5–16.6	13.7–16.0	13.0–14.7
Gill V	18.1–22.2	18.6–21.6	18.9–21.5	18.0–20.4	16.4–18.0
Origin pectoral	16.4–20.7	16.7–20.0	17.7–19.8	16.2–18.8	15.4–17.2
First dorsal fin	45.7–51.1	46.3–48.5	46.9–53.7	45.5–52.0	44.9–51.8
Pelvic fins	39.6–41.8	40.4–42.1	39.5–44.4	38.9–41.9	33.2–39.5
Anal fin	56.5–60.7	55.7–57.6	54.4–62.5	53.8–61.6	54.2–60.0
Second dorsal fin	62.5–67.5	62.8–64.8	61.8–69.1	63.6–68.9	63 6–69.6
Lower caudal fin	72.3–76.7	71.5–75.0	73.0–77.4	72.7–78.2	73.6–78.5
Upper caudal fin	71.7–78.2	73.6–75.9	74.4–79.3	74.8–79.5	75.2–79.6
Anus	41.0–44.4	43.2–45.5	41.2–51.0	40.1–44.8	37.9–42.2
Length upper caudal fin	21.6–25.4	25.2–28.0	20.7–27.5	19.9–25.2	20.4–24.0
Base first dorsal fin	5.5–7.0	5.8–6.8	5.6–6.7	5.4–6.8	5.9–7.0
Base second dorsal fin	4.5–5.8	5.3–6.3	4.3–5.2	4.4–5.8	4.2–4.7
Base anal fin	7.2–9.1	7.8–9.5	7.2–9.2	7.2–9.3	7.3–9.4
Distance between dorsal fins	10.6–11.9	10.5–11.6	9.2–11.3	10.3–13.7	10.9–14.5
Internasal distance	1.5–2.3	5.8–6.8	1.7–2.7	1.8–2.8	1.6–2.3
Length orbit	3.2–4.3	2.6–3.8	3.1–4.7	2.9–4.3	3.1–3.5
Length lower labial fold	1.3–2.1	1.6–2.3	0.9–1.9	0.4–1.8	1.2–2.0
Length upper labial fold					
Width mouth	6.3–8.1	7.4–8.9	6.9–8.8	5.8–7.8	6.1–7.8
Length mouth	2.8–4.5	3.3–4.3	3.3–4.4	2.8–4.0	3.5–5.5
Height gill I	1.6–2.3	1.1–2.6	1.5–2.5	1.3–1.9	1.6–2.3
Height gill V	0.6–1.2	0.5–1.3	0.6–1.5	0.6–1.2	0.2–1.2
Tip second dorsal to caudal	1.8–3.7	2.7–4.7	1.7–4.2	2.0–4.9	2.7–4.7
Tip pelvic to second dorsal	13.6–15.9	10.5–13.2	9.6–15.4	13.0–16.3	14.7–18.2
Tip pelvic to anal	6.8–10.7	5.8–8.4	4.3–10.2	6.3–11.5	6.2–10.1
Tip pelvic to lower caudal	21.3–25.6	21.1–25.0	20.8–25.4	22.3–26.6	24.6–28.2
Length outer margin pectoral	11.4–15.0	10.9–13.6	10.7–14.9	11.8–13.7	8.5–11.3
Length anterior margin first dorsal	8.1–10.0	8.8–10.6	7.5–10.1	8.0–10.4	7.8–8.6
Length anterior margin second dorsal	5.7–7.7	6.8–8.7	5.7–8.2	5.4–7.9	4.2–5.7
Length anterior margin anal	5.3–8.2	6.8–9.1	5.8–9.2	6.9–8.3	5.5–7.4
Distance eye to spiracle	0.4–1.2	1.1–1.6	0.7–1.5	0.7–1.3	0.7–1.2

TABLE 5.—*Measurements of type specimens of* Schroederichthys, Galeus cadenati *and selected examples of* Galeus arae

Species	*S. maculatus* (type)	*S. tenuis* (type)	*Galeus arae*	*G. arae*	*G. cadenati* (type)
Museum No. or Station No.	USNM 185556	USNM 188052	S.B. 2458	USNM 198104	ORE 3592
	Mm.	*Mm.*	*Mm.*	*Mm.*	*Mm.*
Total length	328	230	290	368	303
Tip of snout to—					
Anterior nasal aperture	8	3	12	14	12
Posterior nasal aperture	11	7	14	18	15
Front mouth	14	9	18	22	20
Eye	15	10	20	25	22
Gill I	43	24	42	59	53
Gill V	53	32	53	75	61
Origin pectoral	50	30	52	73	57
First dorsal fin	126	82	131	156	133
Pelvic fins	100	69	115	144	109
Anal fin	172	120	165	214	151
Second dorsal fin	201	136	183	233	186
Lower caudal fin	260	179	210	270	210
Upper caudal fin	265	182	206	267	210
Anus	104	71	126	162	120
Length upper caudal fin	60	38	85	100	90
Base first dorsal fin	14	10	14	17	17
Base second dorsal fin	18	15	14	17	16
Base anal fin	24	21	30	32	45
Distance between dorsal fins	65	42	36	61	39
Internasal distance	8	6	8	11	8
Length orbit	11	7	10	13	9
Length lower labial fold	4	4	5	8	5.5
Length upper labial fold	4	3	3	5	4
Width mouth	19	13	20	26	21
Length mouth	11	6	12	15	12
Height gill I	5	4	5	6	4
Height gill V	2	2	3	3	3
Tip second dorsal to caudal	36	24	3	10	5
Tip pelvic to second dorsal	71	47	37	49	31
Tip pelvic to anal	42	30	20	24	2
Tip pelvic to lower caudal	135	92	63	81	59
Length outer margin pectoral	32	22	31	42	42
Length anterior margin first dorsal	23	18	21	29	30
Length anterior margin second dorsal	29	20	21	24	25
Length anterior margin anal	18	14	16	23	26
Distance eye to spiracle	3	2	3	4	4

TABLE 6.—*Range of total lengths and measurements expressed as percent of total length in* Schroederichthys *and* Galeus

Species	*S. maculatus*	*S. tenuis*	*Galeus arae*	*G. arae*	*G. cadenati*	*G. melastomus*
Number of specimens measured	49	2	10	1	10	5
Length range in millimeters	145–342	180–230	190–321	269–368	273–348	313–635
Tip of snout to—	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*
Anterior nasal aperture	1.4– 2.4	1.3– 1.7	3.1– 4.1	3.4– 3.9	3.2– 5.1	3.2– 4.8
Posterior nasal aperture	2.4– 3.9	3.0– 3.3	4.3– 5.2	4.5– 5.2	4.6– 5.8	4.2– 6.7
Front mouth	3.1– 4.7	3.9– 3.9	5.3– 7.1	6.0– 6.9	6.0– 7.3	6.3– 8.6
Eye	3.7– 5.2	4.4– 4.4	5.3– 7.5	5.9– 7.8	6.3– 7.6	6.3– 8.3
Gill I	9.9–13.1	10.4–11.1	13.8–16.0	14.9–16.7	15.5–18.5	12.6–17.5
Gill V	12.9–17.0	13.9–14.4	16.3–19.8	20.1–20.7	18.2–22.2	17.2–23.0
Origin pectoral	12.0–16.3	13.0–13.3	15.3–19.3	19.0–20.1	16.7–21.8	16.7–22.1
First dorsal fin	34.7–40.8	34.4–35.6	42.4–47.3	40.9–43.4	43.2–47.9	44.9–48.2
Pelvic fins	28.9–33.6	29.4–30.0	37.2–42.0	34.6–39.1	34.5–40.2	36.9–39.6
Anal fin	49.4–54.5	49.4–52.2	50.9–56.9	52.7–58.2	49.8–55.6	52.1–53.9
Second dorsal fin	58.3–62.6	57.2–59.2	59.0–67.7	59.8–63.3	60.1–64.7	61.5–63.9
Lower caudal fin	77.5–82.8	77.7–77.8	68.8–74.1	68.8–74.7	69.0–75.1	69.4–70.6
Upper caudal fin	79.3–83.5	79.1–79.4	67.5–72.0	68.4–74.5	69.3–75.1	70.0–72.5
Anus	28.7–36.4	30.5–30.9	39.8–46.3	39.8–44.0	39.5–45.5	40.3–42.8
Length upper caudal fin	15.9–20.7	16.5–20.5	28.0–31.6	26.2–30.1	24.5–29.7	27.9–30.2
Base first dorsal fin	3.5– 5.1	4.4– 4.4	4.2– 5.9	4.3– 5.1	4.9– 6.3	4.4– 5.1
Base second dorsal fin	5.2– 8.1	6.1– 6.5	4.4– 5.7	4.1– 5.2	5.0– 6.3	4.6– 5.4
Base anal fin	6.6– 9.0	7.8– 9.1	10.3–13.6	8.7– 9.5	13.2–15.0	12.8–15.5
Distance between dorsal fins	17.2–20.0	18.3–19.4	11.3–12.9	14.1–16.6	12.3–14.7	10.9–14.0
Internasal distance	1.9– 2.5	2.4– 2.5	2.5– 3.3	3.0– 3.3	2.4– 3.2	2.4– 3.5
Length orbit	2.7– 3.5	3.0– 3.1	3.4– 3.9	3.1– 3.7	3.0– 4.0	3.6– 4.5
Length lower labial fold	0.8– 1.7	1.7– 1.7	1.4– 2.2	1.7– 2.6	1.6– 2.2	1.3– 1.9
Length upper labial fold	0.6– 1.2	1.3– 1.7	1.0– 1.5	1.4– 2.0	1.3– 1.7	1.0– 1.6
Width mouth	5.2– 6.8	5.7– 6.1	6.2– 7.5	7.1– 9.2	6.6– 9.1	6.2– 7.9
Length mouth	1.8– 3.9	2.6– 2.8	3.2– 4.3	3.0– 4.1	3.2– 5.5	3.3– 5.4
Height gill I	1.2– 2.1	1.1– 1.7	1.3– 2.1	1.1– 1.7	1.3– 2.1	1.9– 2.8
Height gill V	0.3– 0.7	0.4– 0.7	0.6– 1.3	0.6– 1.1	0.7– 1.3	0.9– 1.4
Tip second dorsal to caudal	9.6–12.9	10.4–12.2	0.2– 1.5	1.5– 2.7	0.0– 2.2	0.5– 1.3
Tip pelvic to second dorsal	18.4–23.1	19.4–20.4	8.8–12.6	10.4–13.3	9.8–11.9	10.2–14.2
Tip pelvic to anal	9.3–13.4	12.2–13.1	1.6– 6.7	4.8– 7.1	0.7– 3.2	1.3– 3.6
Tip pelvic to lower caudal	37.2–42.0	40.0–40.0	18.4–21.7	19.7–22.0	17.9–22.6	19.5–20.4
Length outer margin pectoral	8.2–11.8	9.4– 9.6	10.5–12.2	9.9–11.9	12.9–15.6	11.9–13.2
Length anterior margin first dorsal	6.1– 8.4	7.2– 7.8	7.2– 8.3	6.3– 7.9	8.5–10.5	7.7– 8.9
Length anterior margin second dorsal	6.8– 9.9	8.7– 8.9	7.0– 8.0	6.1– 6.9	7.9– 9.2	7.6– 8.9
Length anterior margin anal	3.4– 6.8	6.1– 7.2	5.5– 8.0	5.7– 6.2	6.4– 8.6	6.4– 8.1
Distance eye to spiracle	0.5– 1.5	0.8– 0.9	0.8– 1.5	0.9– 1.5	1.1– 1.4	0.7– 1.3

TABLE 7.—*Measurements of a type specimen of* Apristurus *and of selected examples of* Apristurus *and* Halaelurus

Species Museum No. or other designation	*A. profundorum* MCZ 38299	*A. indicus* ORE 3654	*A. riveri* ORE 3586	*A. laurussoni* MCZ 38406	*H. bivius* Coast Chile 42° S.	*H. chilensis* Coast Chile 30° S.
	Mm.	*Mm.*	*Mm.*	*Mm.*	*Mm.*	*Mm.*
Total length	390	303	430	540	625	365
Tip of snout to—						
Anterior nasal aperture	21	18	20	24	----	----
Posterior nasal aperture	34	25	30	36	----	----
Front mouth	40	31	35	46	22	12
Eye	46	33	46	52	----	----
Gill I	85	67	85	110	100	55
Gill V	104	78	109	130	128	68
Origin pectoral	99	76	105	124	120	64
First dorsal fin	170	152	210	252	270	140
Pelvic fins	150	125	180	230	----	----
Anal fin	192	151	230	295	----	----
Second dorsal fin	212	185	270	338	----	----
Lower caudal fin	243	206	296	378	----	----
Upper caudal fin	253	210	308	390	509	293
Anus	164	139	195	257	250	135
Length upper caudal fin	115	93	123	148	116	72
Base first dorsal fin	23	12	17	35	39	27
Base second dorsal fin	29	17	27	35	42	32
Base anal fin	57	53	61	85	62	29
Distance between dorsal fins	28	25	33	47	100	50
Internasal distance	18	14	17	20	17	8
Length orbit	13	10	15	16	17	10
Lenth lower labial fold	15	6	12	14	17	8
Length upper labial fold	11	10	10	19	20	8
Width mouth	34	23	23	48	40	27
Length mouth	20	11	20	24	25	13
Height gill I	7	3	11	9	10	6
Height gill V	7	2	8	5	6	4
Tip second dorsal to caudal	−10	−3	----	----	----	----
Tip pelvic to second dorsal	30	27	38	44	----	----
Tip pelvic to anal	----	−4	8	----	----	----
Tip pelvic to lower caudal	56	49	70	85	----	----
Length outer margin pectoral	40	34	48	70	76	45
Length anterior margin first dorsal	34	15	27	50	64	40
Length anterior margin second dorsal	45	25	36	50	68	45
Length anterior margin anal	20	22	30	50	47	27
Distance eye to spiracle	6	3	4	6	----	----

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TABLE 8.—*Range of total lengths and measurements expressed as percent of total length in* Apristurus *and* Halaelurus

Species	*A. profundorum*	*A. indicus*	*A. riveri*	*A. laurussoni*	*H. bivius*	*H. chilensis*
Number of specimens measured	5	12	6	10	2	2
Length range in millimeters	230–390	235–475	338–460	212–580	555–625	365–392
Tip of snout to—	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*	*Percent*
Anterior nasal aperture	4.8– 7.2	4.2– 5.9	4.7– 6.3	3.8– 5.4		
Posterial nasal aperture	7.4–10.4	6.6– 9.3	6.5– 8.3	6.1– 8.3		
Front mouth	8.7–10.9	7.6–11.2	7.4–10.0	7.5– 9.6	3.5– 3.8	3.3– 3.3
Eye	10.9–13.0	8.4–11.9	10.0–11.8	8.0–11.5		
Gill I	19.1–22.8	16.8–22.0	18.3–21.3	17.0–21.4	15.1–16.0	15.2–16.6
Gill V	23.5–26.7	21.5–25.8	22.2–25.3	22.2–26.8	18.4–20.5	18.3–21.4
Origin pectoral	23.0–25.4	20.2–25.1	21.0–24.4	21.6–25.8	18.0–19.2	17.5–20.4
First dorsal fin	40.9–43.6	47.9–51.8	45.6–48.9	43.4–51.2	40.5–43.2	38.4–38.6
Pelvic fins	38.3–41.6	38.2–42.7	39.4–42.7	40.1–47.8		
Anal fin	46.1–50.8	49.5–53.6	47.9–53.6	47.5–57.9		
Second dorsal fin	53.9–58.3	58.5–63.6	56.8–62.8	59.0–67.2		
Lower caudal fin	61.3–64.4	65.6–71.8	64.5–68.8	63.6–72.4		
Upper caudal fin	64.8–66.9	67.2–72.6	65.1–71.6	66.0–79.3	78.0–81.4	74.7–80.3
Anus	42.0–44.3	42.8–49.6	43.5–47.7	42.9–51.2	37.9–40.0	37.0–38.2
Length upper caudal fin	29.5–33.5	29.3–32.2	28.3–32.1	25.9–31.0	18.6–22.0	19.7–20.2
Base first dorsal fin	4.8– 7.0	3.4– 4.8	3.3– 4.4	4.5– 6.6	5.6– 6.2	7.4– 7.7
Base second dorsal fin	6.5– 7.4	5.0– 6.8	5.4– 6.8	4.8– 7.3	6.7– 8.3	8.8– 9.2
Base anal fin	13.2–14.8	13.5–18.3	13.0–18.0	13.8–16.9	9.4– 9.9	7.9– 8.9
Distance between dorsal fins	6.0– 9.6	6.0– 8.8	5.9– 8.9	8.7–10.8	16.0–16.2	16.4–16.6
Internasal distance	3.6– 4.8	3.7– 4.7	3.7– 4.3	3.6– 5.0	2.3– 2.7	2.0– 2.2
Length orbit	2.2– 3.3	2.5– 4.0	3.3– 3.5	2.7– 3.9	2.7– 2.9	2.7– 2.8
Length lower labial fold	2.0– 3.8	1.6– 2.6	2.2– 2.8	2.1– 3.2	2.2– 2.7	2.2– 2.6
Length upper labial fold	1.6– 2.8	1.9– 3.9	2.2– 2.7	3.1– 3.9	2.7– 3.2	2.2– 2.6
Width mouth	5.7– 8.7	6.3– 9.4	5.3– 7.3	6.1–10.0	5.8– 6.4	7.4– 7.7
Length mouth	3.9– 5.1	3.3– 4.8	3.2– 5.2	3.3– 5.9	5.0– 5.6	3.6– 3.6
Height gill I	0.9– 2.0	1.0– 2.2	2.2– 2.6	0.8– 2.3	1.4– 1.6	1.6– 2.0
Height gill V	0.9– 1.6	0.4– 1.3	0.9– 1.9	0.5– 1.1	0.7– 1.0	0.1– 1.3
Tip second dorsal to caudal		0 – 1.3	0 – 3.5	0 – 1.8		
Tip pelvic to second dorsal	5.2– 9.3	6.7–12.6	7.4–11.5	6.6–10.8		
Tip pelvic to anal	−3.0– 2.0	−1.5– 2.5	0 – 2.0	0 – 1.7		
Tip pelvic to lower caudal	13.0–16.2	14.9–18.1	14.8–16.3	14.1–18.4		
Length outer margin pectoral	8.8–10.9	8.4–11.6	9.8–11.9	8.3–13.0	11.7–12.2	12.0–12.3
Length anterior margin first dorsal	7.0– 8.9	5.2– 7.5	5.4– 7.4	7.1– 9.3	9.0–10.2	10.4–11.0
Length anterior margin second dorsal	7.8–11.5	7.2– 9.7	8.4–11.0	7.4– 9.9	10.9–12.6	12.0–12.3
Length anterior margin anal	5.1– 6.0	5.8– 9.1	6.5– 8.1	7.1– 9.3	7.4– 7.5	7.4– 8.2
Distance eye to spiracle	0.9– 1.6	0.8– 1.3	0.9– 1.2	0.9– 1.2		

A look at the literature on scyliorhinids of the Indo-Pacific and an examination of very few specimens suggests that studies of Indo-Pacific species will provide a better basis for estimates of phylogenetic relationhips than can be made from Atlantic species alone. The Atlantic material does suggest, however, that more detailed study of dentition would be desirable, especially with attention to tooth development. For this review no positive evidence on scyliorhinid migration and very little information on habit patterns were found. Further studies of species found in the higher latitudes off South America appear most promising for estimating the course of scyliorhinid phylogeny.

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Work on this paper was started in 1957 when the intention was to describe a new species of *Scyliorhinus* from the single specimen of that species then known. An illustration of this specimen was prepared at the time by Nancy Mead and is used here. Additional material became available later, requiring description of other new species. Illustrations of several of these were prepared by Mildred Carrington. With a decision to expand the paper to cover catsharks of the western Atlantic region, other illustrations were prepared by Mary Wagner.

Examinations of type material by Dr. Daniel M. Cohen and radiographs prepared by staff technicians at the Bureau of Commercial Fisheries Ichthyological Laboratory in Washington, D.C., helped me reach an opinion on the status of *Apristurus profundorum* (Goode and Bean).

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SURVEY OF PELAGIC FISHES OF THE CALIFORNIA CURRENT AREA

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ABSTRACT

The pelagic fishes off central California to central Baja California were surveyed with four kinds of nekton-collecting nets. Construction and operation of one of these nets, the collapsible midwater beam trawl, are described. The survey was made during eight cruises between May 1961 and March 1963. More than 189 fish species and about 52,000 specimens were taken. The number and size range of specimens at each station of capture are listed for all the species; charts of the location of capture are given for most species; and several species are illustrated. The records for many of the species are annotated with remarks and data on taxonomy, range, ecology, and ontogeny.

A survey of the nekton off central California to central Baja California was begun in January 1962 by the Life History and Taxonomy Program of the Bureau of Commercial Fisheries, California Current Resources Laboratory, La Jolla, Calif. The purpose of this survey was twofold: to begin to learn what larger pelagic organisms (primarily fishes) occur in the area sampled and to investigate certain aspects of the life history of the hake (*Merluccius*), a species of potential commercial importance. This report presents a list of the more than 189 species of fishes taken on the survey, with annotations on life history, distribution, and taxonomy for many of the species. A subsequent report will give data obtained on the hake other than records of occurrence. The invertebrates collected were placed in the Marine Invertebrate Collection of Scripps Institution of Oceanography.

Since development of the Isaacs-Kidd midwater trawl (IKMWT) in 1950, a large number of tows have been made in the Pacific with this type of net (Aron, 1960; King and Iversen, 1962; Clarke, 1963). Specimens collected with the IKMWT have been deposited in various museums, but only the collections made by Aron (1960) have been reported comprehensively. Wisner (1962) gave a list of species and numbers of each taken in 14 IKMWT tows during Operation "Wigwam" off Baja California.

In addition to the 10-ft. IKMWT, this survey used a 10- by 14-ft. collapsible midwater beam trawl (CMWBT), to be described in a later section, a 5- by 5-ft. nekton net (Blackburn, 1960: 53–55), and the large *Cobb* Mark–II pelagic trawl of about 70- by 80-ft. mouth opening (McNeely, 1963).

After examining the catches made by the various nets, it seems obvious that none of the nets used is adequate by itself to sample the nekton of the bathypelagic area and that a variety of nets should be used in future surveys. The *Cobb* trawl, because of its large size, is more efficient than other nets used in catching the larger and more elusive organisms. Direct comparisons of the catching efficiencies of these nets are not made in this report, because of the many variables that entered into the survey.

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CRUISES

This report has used the collections from eight cruises made from May 1961 through March 1963 (table 1). Four cruises were made by the Bureau's R/V *Black Douglas* (B6203, B6204, B6212, and B6303); two by the R/V *John N. Cobb* through cooperation of the Bureau of Commercial Fisheries Exploratory Fishing Base, Seattle, Wash. (C6208 and C6303); and two cruises by the R/V *Horizon* through cooperation of Scripps Institution of Oceanography (H6105 and H6204). The cruises are briefly summarized below. The stations at which no fish were caught are listed below as "negative tows." The depths of tows in meters and the number of tows (in parentheses) follow the information on the types of nets used.

Cruise H6105: R/V *Horizon;* May 27–28, 1961; 135 to 160 km. (85 to 100 miles) west of San Diego, Calif.; 5 tows with IKMWT: 18 (2), 178 (1), 705–1,093 (2).

Cruise B6203: R/V *Black Douglas;* March 2–30, 1962; San Francisco, Calif., to south-central Baja California, up to 970 km. (600 miles) seaward; 29 tows with CMWBT and 2 tows with 5- x 5-ft. nekton net: 9–132 (6), 256–264 (9), 419–423 (15), 622 (1); negative tows, stations 70.80a, 70.130, 80.51, 80.80, 90.150; other cruise work, oblique tows with 1-m. standard plankton nets and 2-m. stramin nets, bottom trawls with 16-ft. otter trawls.

Cruise H6204: R/V *Horizon;* March 16 to April 24, 1962; San Francisco, Calif., to Cedros Island, Baja California, up to 970 km. (600 miles) seaward; 48 tows with IKMWT: 148 (1), 298 (25), 410 (1), 1,490 (1), 1,676 (14), 1,863 (4), 2,234 (2).

Cruise B6204: R/V *Black Douglas;* April 6–7, 1962; 16 to 19 km. (10 to 12 miles) SW. of San Diego, Calif.; 6 tows with CMWBT: 38 (3), 282 (1), 564 (2); other cruise work, oblique tows with 1-m. standard plankton net.

Cruise C6208: R/V *John N. Cobb;* August 6 to September 7, 1962; San Francisco, Calif., to Ensenada, Baja California, up to 970 km. (600 miles) seaward; 61 tows with *Cobb* pelagic trawl Mark II: surface–92 (34), 183–296 (4), 366–403 (23); negative tows, stations 90.49a, 91.39c.

TABLE 1.—*Pelagic survey station data*

[Asterisks indicate that values are approximate]

Station	Vessel and cruise	Sequence occupied	Location of haul				Date	Time of tow (P.s.t.)		Depth of bottom	Towing wire out	Depth fished	Type of haul
			Start		End			Start	End				
			Lat. N.	Long. W.	Lat. N.	Long. W.							
								Hour	*Hour*	*M.*	*M.*	*M*	
60.55	C6208	91	37°45.5′	123°20.3′	37°42.0′	123°23.8′	6 Aug. 1962	1750	2000	1, 189–2, 379	1, 052	*366	Oblique.
60.60	H6204	39	37°36.6′	123°37.0′			26–27 Mar. 1962	2024	0005	3, 331	5, 032	*1, 863	Horizontal.
60.60	C6208	92	37°37.0′	123°37.0′	37°42.2′	123°34.0′	7 Aug. 1962	0655	0915	3, 111–2, 928	1, 052	*366	Oblique.
60.70	H6204	41	37°07.9′	124°25.0′			27 Mar. 1962	0613	0750	3, 843	805	*298	Horizontal.
60.70	C6208	93	37°22.2′	124°12.3′	37°17.8′	124°15.0′	7 Aug. 1962	1440	1657	3, 843	1, 052	*366	Oblique.
60.80	H6204	42	36°54.0′	125°04.4′			27 Mar. 1962	1250	2000	4, 117	6, 039	*2, 234	Horizontal.
60.80	C6208	94	36°55.5′	125°04.0′	37°03.5′	124°59.0′	7–8 Aug. 1962	2225	0025	4, 209	1, 052	*366	Oblique.
60.90	H6204	43	36°34.4′	125°46.0′			28 Mar. 1962	0012	0147	4, 392	805	*298	Horizontal.
60.90	C6208	95	36°36.0′	125°38.4′	36°38.6′	125°34.0′	8 Aug. 1962	0655	0905	4, 484	1, 052	*366	Oblique.
60.100	H6204	45	36°17.0′	126°31.0′			28 Mar. 1962	0809	1226	4, 502	4, 032	*1, 863	Horizontal.
60.100	C6208	96	36°15.0′	126°32.0′	36°12.8′	126°25.0′	8 Aug. 1962	1545	1800	4, 575	1, 052	*366	Oblique.
60.120	B6203	20	35°27.2′	128°00.0′			13 Mar. 1962	0035	0400	4, 575	604	*1, 419	Do.
60.120	H6204	46	35°35.2′	127°54.0′			28–29 Mar. 1962	2205	0010	3, 697	805	*298	Horizontal.
60.140	H6204	48	34°57.0′	129°19.0′			29 Mar. 1962	1022	1511	4, 602	5, 032	*1, 863	Do.
60.160	B6203	21	34°19.0′	130°39.5′			13–14 Mar. 1962	2310	0210	5, 124	604	*423	Oblique.
60.160	H6204	50	34°16.0′	130°41.5′			29–30 Mar. 1962	2330	0110	4, 868	805	*298	Horizontal.
60.180	B6203	22	33°40.5′	132°00.0′			14 Mar. 1962	1140	1425	5, 124	604	*423	Do.
60.180	H6204	51	33°38.0′	131°54.0′			30 Mar. 1962	1300	1650	4, 826	4, 026	*419	Do.
60.200a	B6203	23	32°56.8′	133°26.8′			15 Mar. 1962	0050	0400	4, 941	604	*423	Oblique.
60.200b	B6203	24	32°56.8′	133°26.8′			15 Mar. 1962	0400	0520	4, 941	92	*31	Do.
60.200	H6204	52	32°55.0′	133°28.0′			31 Mar. 1962	0255	0425	5, 051	805	*298	Horizontal.
65.54	C6208	105	37°05.0′	122°34.0′	36°59.0′	122°32.5′	15 Aug. 1962	0044	0145	110–275	92	24	Do.
66.50a	C6208	102	36°57.0′	122°10.5′	36°55.5′	122°07.0′	11 Aug. 1962	0044	0144	55	47	24	Do.
66.50b	C6208	103	36°58.0′	122°09.8′	36°57.0′	122°07.0′	11 Aug. 1962	0330	0430	31	47	24	Do.
66.100	C6208	97	35°29.0′	125°51.2′	35°23.0′	125°52.4′	8–9 Aug. 1962	2325	0125	4, 575	183	*46	Do.
66.50	C6208	104	36°43.0′	121°58.5′	36°42.0′	121°58.0′	13 Aug. 1962	0841	0912	183–92	366	*92	Do.
70.51	C6208	106	36°10.5′	121°48.0′	36°08.0′	121°47.0′	15 Aug. 1962	1432	1532	238–677	686	201	Do.
70.60	C6208	101	35°14.0′	123°52.0′	35°07.5′	123°58.5′	9–10 Aug. 1962	2312	0112	4, 118	1, 052	*366	Oblique.
70.80a	B6203	17	35°13.5′	123°47.0′			6 Mar. 1962	1930	2300	4, 026	604	*256	Do.
70.80b	B6203	18	35°13.5′	123°47.0′			6 Mar. 1962	2300	2400	4, 026	121	*29	Horizontal.
70.80–5m	B6203	19	35°18.0′	123°44.0′			7 Mar. 1962	0040	0235	4, 026	92	*9	Do.
70.80	C6208	100	35°14.0′	123°52.0′	35°07.5′	123°58.5′	9–10 Aug. 1962	2312	0112	4, 118	47	24	Do.
70.90	B6203	16	34°53.0′	124°30.0′			6 Mar. 1962	1050	1455	4, 209	604	*256	Oblique.
70.90	C6208	99	34°53.0′	124°33.0′	34°47.0′	124°31.0′	9 Aug. 1962	1520	1720	4, 209	47	24	Horizontal.
70.100	C6208	98	34°34.0′	125°15.0′	34°30.0′	125°12.0′	9 Aug. 1962	0810	1020	4, 667	1, 052	*366	Oblique.
70.130	B6203	15	33°39.0′	127°00.0′			5 Mar. 1962	1200	1520	3, 660	604	*423	Do.
70.—	H6204	53	31°15.0′	132°07.8′			31 Mar. 1962	1905	2330	4, 694	4, 529	*1, 676	Horizontal.

TABLE 1.—*Pelagic survey station data*—Continued

Station	Vessel and cruise	Sequence occupied	Location of haul				Date	Time of tow (P.s.t.)		Depth of bottom	Towing wire out	Depth fished	Type of haul
			Start		End			Start	End				
			Lat. N.	Long. W.	Lat. N.	Long. W.		Hour	Hour	M.	M.	M.	
73.200	B6203	25	30°38.0′	131°53.2′			15–16 Mar. 1962	2310	0210	4, 758	604	*423	Do.
77.51	C6208	107	35°01.5′	121°00.0′	34°59.4′	120°59.3′	16 Aug. 1962	0033	0133	348–366	110	*13	Do.
79.54	B6303	163	34°32.0′	120°50.5′	34°30.5′	120°53.2′	1 Mar. 1963	1513	1640	503	600	*386	Oblique.
80.51	B6203	6	34°26.5′	120°32.8′			2 Mar 1962	1750	2110	119	132	*92	Do.
80.52	C6208	112	34°22.3′	120°44.0′	34°18.0′	120°43.5′	20 Aug. 1962	0227	0447	458–686		*24	Horizontal.
80.52	C6303	164	34°31.8′	120°40.2′	34°29.4′	120°37.7′	1 Mar. 1963	1800	1955	77–81	92	*27	Do.
80.55	H6204	26	34°18.6′	120°48.0′			16 Mar. 1962	1927	2135	695	805	*298	Do.
80.60	B6203	7	34°10.0′	121°09.7′			2–3 Mar. 1962	2340	0235	2, 196	377	*264	Oblique.
80.60	H6204	28	34°06.6′	121°08.0′			17 Mar. 1962	0100	0236	2, 196	805	*298	Horizontal.
80.60	C6208	113	34°09.5′	121°11.0′	34°05.8′	121°08.0′	20 Aug. 1962	0850	1100	2, 196	1, 052	*366	Oblique.
80.60	C6303	165	34°11.1′	121°10.0′	34°06.1′	121°04.4′	4 Mar. 1963	1550	1830	1, 501	648	*201	Horizontal.
80.65	B6303	166	33°59.0′	121°30.5′	33°53.2′	121°27.7′	4 Mar. 1963	2011	2140	3, 294	150	*55	Oblique.
80.70	B6203	8	33°49.2′	121°51.8′			3 Mar. 1962	0830	0935	3, 660	377	*264	Do.
80.70	H6204	29	33°54.0′	121°50.0′			17 Mar. 1962	0948	1424	4, 260	5, 032	*1, 863	Horizontal.
80.70	C6208	114	33°48.7′	121°51.0′	33°42.5′	121°49.7′	20 Aug. 1962	1600	1813	3, 660	1, 052	*366	Oblique.
80.70	C6303	167	33°40.0′	121°54.4′	33°44.0′	121°49.7′	4–5 Mar. 1963	2302	0125	5, 569	64	22	Horizontal.
80.75	B6303	168	33°39.0′	122°11.5′	33°34.7′	122°29.0′	5 Mar. 1963	0445	0725	3, 660			Oblique.
80.80	B6203	9	33°28.7′	122°32.6′			3 Mar. 1962	1405	1635	3, 660	377	*264	Do.
80.80	H6204	30	33°33.0′	122°35.0′			17 Mar. 1962	2045	2230	4, 209	805	*298	Horizontal.
80.80	C6208	115	33°26.0′	122°30.0′	33°21.0′	122°29.0′	20–21 Aug. 1962	2320	0120	4, 392		24	Do.
80.80	C6303	169	33°30.0′	122°38.0′	33°22.3′	122°38.2′	5 Mar. 1963	0605	0850	4, 026	640	*183	Do.
80.90	B6203	10	33°09.0′	123°14.0′			3 Mar. 1962	2030	2200	4, 392	377	*264	Oblique.
80.90–5n	B6203	11	33°07.0′	123°15.0′			3 Mar. 1962	2300	2400	4, 392	92	*9	Horizontal.
80.90	H6204	32	33°13.1′	123°16.0′			18 Mar. 1962	0500	1050	4, 172	6, 039	*2, 234	Do.
80.100	B6203	12	32°49.0′	123°55.0′			4 Mar. 1962	0330	0635	3, 660	377	*264	Oblique.
80.100	H6204	33	32°57.0′	123°56.0′			18 Mar. 1962	1512	1654	3, 935	805	*298	Horizontal.
80.110	B6203	13	32°28.3′	124°36.2′			4 Mar. 1962	0930	1150	4, 392	377	*264	Oblique.
80.120	B6203	14	32°08.7′	125°17.8′			4 Mar. 1962	1630	1915	4, 209	377	*264	Do.
80.130	C6208	116	31°55.0′	126°06.0′	31°50.0′	126°07.5′	22 Aug. 1962	0600	0700	4, 392	128	24	Horizontal.
80.140	C6208	117	31°26.0′	126°39.0′	31°24.0′	126°40.0′	22 Aug. 1962	1110	1245	4, 392	1, 200	*403	Oblique.
80.150	C6208	118	31°10.0′	127°17.5′	31°06.0′	127°18.0′	22 Aug. 1962	1750	1925	4, 392	1, 200	*403	Do.
80.160	C6208	119	30°50.0′	127°57.0′	30°47.0′	127°55.0′	22–23 Aug. 1962	2250	0050	4, 026		24	Horizontal.
80.170	C6208	120	30°30.0′	128°36.0′	30°27.0′	128°38.0′	23 Aug. 1962	0652	0825	4, 392	1, 200	*403	Oblique.
80.180	C6208	121	30°07.0′	129°16.0′	30°05.0′	129°19.0′	23 Aug. 1962	1135	1315	4, 392	1, 200	*403	Do.
80.190	C6208	122	29°49.0′	129°55.0′	29°46.0′	129°54.0′	23 Aug. 1962	1835	1935	4, 392		24	Horizontal.
80.200	H6204	54	29°29.0′	130°36.0′			1 Apr. 1962	1358	1535	4, 502	805	*298	Do.
80.210	C6208	123	29°29.0′	130°36.0′	29°26.0′	130°34.0′	23–24 Aug. 1962	2350	0140	4, 392	1, 200	*403	Oblique.
82.45	C6208	108	34°18.0′	119°55.0′	34°18.0′	119°53.0′	16 Aug. 1962	1951	2051	458		18	Horizontal.
82.60	C6303	191	33°26.3′	121°27.1′	33°23.8′	121°24.0′	13 Mar. 1963	1947	2140	3, 660	549	*165	Do.
83.70	C6303	183	33°12.0′	121°26.7′	33°08.5′	121°26.0′	8 Mar. 1963	1810	2130	4, 026	686	*183	Do.
83.70a	B6303	184	33°18.0′	121°32.0′	33°13.5′	121°27.5′	8 Mar. 1963	1933	2064	4, 026	300	*113	Do.
83.70b	B6303	185	33°12.5′	121°27.5′	33°11.5′	121°25.2′	8 Mar. 1963	2058	2215	4, 026	80	18	Do.
83.70c	B6303	186	33°11.5′	121°25.2′	33°09.0′	121°20.2′	8–9 Mar. 1963	2219	0020	4, 026	400	*168	Do.
83.72	B6303	188	33°10.7′	121°30.0′	33°04.8′	121°25.0′	9 Mar. 1963	0850	1115	3, 660	600	*201	Do.
83.77	C6303	172	33°04.0′	121°58.8′	32°58.0′	121°55.5′	6 Mar. 1963	0800	1015	3, 843	1, 464	*489	Do.
83.90	C6303	170	32°37.7′	122°47.2′	32°31.4′	122°49.3′	5 Mar. 1963	1400	1700	3, 843	1, 144	*366	Do.
84.67	C6303	192	33°12.8′	121°11.0′	33°09.5′	121°08.2′	13 Mar. 1963	1517	1710	3, 294	961	*238	Oblique.
84.68	C6303	191	33°12.3′	121°12.0′	33°09.3′	121°09.5′	13 Mar. 1963	1243	1420	3, 477	824	*247	Horizontal.
84.70	C6303	187	33°06.5′	121°21.5′	33°00.0′	121°19.0′	8–9 Mar. 1963	2350	0300	4, 026	824	*220	Do.
84.71	C6303	182	33°09.0′	121°28.0′	33°05.0′	121°26.5′	8 Mar. 1963	1310	1530	4, 026	1, 098	*311	Oblique.
84.92	B6303	171	32°19.0′	122°52.0′	32°14.0′	122°48.0′	6 Mar. 1963	0305	0525	3, 660	700	*311	Do.
85.68	C6303	189	33°05.0′	121°12.0′	33°03.0′	121°07.0′	9 Mar. 1963	1410	1630	2, 562	869	*238	Horizontal.
86.92	C6303	175	32°07.3′	122°39.5′	32°00.5′	122°41.4′	6 Mar. 1963	1617	1945	4, 209	1, 738	*640	Do.
87.70a	B6303	162	32°29.3′	121°09.0′	32°32.0′	121°04.0′	28 Feb. 1963	0645	0845	3, 843	650	*274	Oblique.
87.70b	B6303	194	33°14.0′	121°22.0′			18 Mar. 1963	0825	1540	3, 843	800		Do.
87.80	C6303	181	32°17.0′	121°44.0′	32°20.8′	121°45.5′	8 Mar. 1963	0525	0755	3, 843	1, 738	*640	Horizontal.
87.90	C6303	176	31°40.5′	122°03.5′	31°37.0′	122°04.3′	6–7 Mar. 1963	2238	0020	4, 026	64	16	Do.
87.200	B6203	27	28°20.0′	130°22.0′			16–17 Mar. 1962	2035	0100	4, 758	604	*423	Oblique.
88.105a	B6303	173	31°06.9′	123°12.2′	31°04.6′	123°07.5′	6 Mar. 1963	1313	1525	4, 026	800	*311	Do.
88.105b	B6303	174	31°04.6′	123°07.5′	31°03.0′	123°02.0′	6 Mar. 1963	1537	1756	4, 026	800	*320	Horizontal.
90.32	B6203	38	33°20.2′	118°05.3′			22 Mar. 1962	0953	1501	769–549	800	*622	Oblique.
90.32	H6204	65	33°19.0′	118°02.7′			6–7 Apr. 1962	2320	0215	787	800	*298	Horizontal.
90.35	B6203	37	33°21.0′	118°18.3′			22 Mar. 1962	0345	0440	86	190	86	Do.
90.45a	H6105	4	32°45.0′	118°48.6′	33°00.1′	119°05.2′	27–28 May 1961	2335	0505	1, 391–1, 684	1, 812	1, 093	Do.
90.45b	H6105	5	33°00.9′	119°08.3′	32°48.1′	118°44.1′	28 May 1961	0535	1015	1, 510	30	18	Do.
90.45	H6204	63	32°55.5′	118°54.5′			6 Apr. 1962	1605	1735	1, 720	800	*298	Do.
90.47	C6208	110	32°49.0′	119°08.0′	32°46.5′	118°57.0′	17 Aug. 1962	1507	1807	1, 007–1, 373	1, 052	*366	Oblique.
90.48a	H6105	1	32°49.6′	119°05.7′	32°53.4′	119°09.5′	27 May 1961	1055	1400	842	1, 006	*704	Horizontal.
90.48b	H6105	2	32°46.0′	119°05.4′	32°51.4′	119°10.7′	27 May 1961	1500	1720	842	251	178	Do.
90.48c	H6105	3	32°44.4′	119°05.1′	32°49.0′	119°10.0′	27 May 1961	1845	2100	641	49	18	Do.
90.49a	C6208	109	32°46.0′	119°12.0′	32°44.0′	119°09.0′	17 Aug. 1962			183–55		18	Do.
90.49b	C6208	111	32°46.0′	119°12.0′	32°44.0′	119°09.0′	17 Aug. 1962	2127	2227	183–55		18	Do.
90.60	B6203	35	32°21.0′	119°46.8′			20–21 Mar. 1962	2315	0305	1, 007	604	*423	Do.
90.60	H6204	61	32°28.5′	120°06.0′			6 Apr. 1962	0450	0620	1, 610	403	*148	Do.
90.60	C6208	134	32°25.0′	119°58.5′	32°22.5′	119°55.0′	28 Aug. 1962	1220	1400	842–915	1, 200	*403	Oblique.
90.70	H6204	60	31°57.0′	120°37.0′			5 Apr. 1962	2100	2240	3, 697	800	*298	Horizontal.
90.70	C6208	133	32°05.0′	120°41.5′	32°03.0′	120°39.0′	28 Aug. 1962	0345	0540	3, 843	1, 200	*403	Oblique.
90.80	C6208	132	31°46.5′	121°33.0′	31°42.0′	121°20.0′	27 Aug. 1962	2013	2215	3, 843		24	Horizontal.
90.90	C6303	180	31°21.0′	122°01.0′	31°33.2′	121°56.0′	7–8 Mar. 1963	2050	0025	4, 118	229	*82	Do.
90.100	C6208	131	31°03.0′	122°32.0′	31°00.0′	122°33.0′	27 Aug. 1962	0945	1140	4, 026	1, 200	*403	Oblique.
90.110	B6203	35	30°42.5′	123°21.2′			19 Mar. 1962	1820	2105	3, 843	600	*423	Horizontal.
90.110	C6303	178	30°47.0′	123°18.8′	30°43.0′	123°20.0′	7 Mar. 1963	0512	0640	4, 392	275	*92	Do.
90.120	H6204	59	30°28.8′	124°06.6′			4 Apr. 1962	1045	1600	4, 081	4, 530	*1, 676	Do.
90.120	C6208	130	30°27.0′	123°59.0′	30°22.0′	124°00.0′	26–27 Aug. 1962	2213	0015	4, 026		24	Do.
90.140	H6204	58	29°42.1′	125°16.0′			3–4 Apr. 1962	2242	0026	4, 264	800	*298	Do.
90.140	C6208	129	29°42.0′	125°21.0′	29°38.0′	125°24.0′	26 Aug. 1962	1030	1230	4, 392	1, 200	*403	Oblique.
90.150	B6203	34	29°25.0′	125°59.5′			18 Mar. 1962	1715	1945	4, 209	600	423	Horizontal.
90.150	C6208	128	29°24.0′	125°57.0′	29°22.0′	126°02.0′	26 Aug. 1962	0245	0445	4, 246		24	Do.
90.160	H6204	57	29°03.0′	126°37.5′			3 Apr. 1962	0810	1223	4, 365	4, 530	*1, 676	Do.

TABLE 1.—*Pelagic survey station data*—Continued

Station	Vessel and cruise	Sequence occupied	Location of haul				Date	Time of tow (P.s.t.)		Depth of bottom	Towing wire out	Depth fished	Type of haul
			Start		End			Start	End				
			Lat. N.	Long. W.	Lat. N.	Long. W.		Hour	Hour	M.	M.	M.	
90.160	C6208	127	29°05.0′	126°38.0′	29°03.0′	126°42.0′	25 Aug. 1962	1930	2110	4,301	1,200	*403	Oblique.
90.180	B6203	31	28°25.0′	127°58.0′			18 Mar. 1962	0020	0200	4,026	600	*423	Horizontal.
90.180	H6204	56	28°22.0′	128°00.0′			2 Apr. 1962	1900	2040	4,484	800	*298	Do.
90.180	C6208	126	28°26.0′	127°57.0′	28°23.0′	128°00.0′	25 Aug. 1962	0600	0740	4,392	1,200	*403	Oblique.
90.190	C6208	125	28°06.5′	128°33.0′	28°03.5′	128°40.0′	24–25 Aug. 1962	2225	0025	4,392		24	Horizontal.
90.200	H6204	55	27°46.0′	129°14.9′			2 Apr. 1962	0534	1006	4,209	4,530	1,676	Do.
90.200	C6208	124	27°46.0′	129°14.0′	27°43.0′	129°16.0′	24 Aug. 1962	1525	1705	4,392	1,200	*403	Oblique.
91.39a	C6208	146	32°53.3′	118°23.8′	32°32.8′	118°23.0′	5 Sept. 1962	2037	2120	732		36	Horizontal.
91.39b	C6208	147	32°52.9′	118°24.0′	32°51.8′	118°22.0′	6 Sept. 1962	0015	0134	366		Surface	Do.
91.39c	C6208	148	32°51.7′	118°22.5′	32°51.5′	118°22.0′	6 Sept. 1962	1005	1030				Do.
92.28	C6208	150	32°59.5′	117°24.0′	33°03.0′	117°24.5′	6 Sept. 1962	2256	2356	458		Surface	Do.
92.115	B6303	177	30°18.8′	123°27.3′	30°12.0′	123°24.0′	7 Mar. 1963	0030	0255	4,026	250	*73	Do.
93.26	C6208	141	33°03.5′	117°19.2′	33°01.5′	117°18.0′	3 Sept. 1962	2017	2130	37–55		36	Do.
93.28	C6208	142	32°58.5′	117°23.0′	33°00.5′	117°24.0′	3–4 Sept. 1962	2315	0015	549		Surface	Do.
93.29	C6208	140	32°53.5′	117°25.0′	32°53.5′	117°27.0′	3 Sept. 1962	0840	1215	549	915	201	Do.
93.31	C6303	190	32°51.1′	117°35.8′	32°49.2′	117°32.3′	12 Mar. 1963	1305	1510	732	915	*274	Do.
93.100	C6303	179	30°31.2′	122°15.7′	30°26.2′	122°09.8′	7 Mar. 1963	1215	1450	4,026	549	*105	Do.
94.28a	C6208	139	32°49.5′	117°20.0′	32°47.5′	117°20.5′	2 Sept. 1962	0115	0215	82		73	Do.
94.28b	C6208	143	32°50.5′	117°20.0′	32°48.0′	117°19.5′	4 Sept. 1962	0230	0400	64		Surface	Do.
94.29a	C6208	135	32°47.0′	117°19.5′	32°45.5′	117°19.0′	31 Aug. 1962	1142	1310	366		296	Do.
94.29b	C6208	136	32°44.0′	117°18.0′	32°46.0′	117°18.5′	1 Sept. 1962	0745	0943	73		*9	Do.
94.29c	C6208	137	32°46.5′	117°18.5′	32°45.0′	117°19.7′	1 Sept. 1962	1913	2022	73–146		*82	Do.
94.29d	C6208	149	32°43.5′	117°17.5′	32°42.0′	117°17.5′	6 Sept. 1962	1715	1820	55		Surface	Do.
94.29e	C6208	151	32°47.0′	117°19.0′	32°44.0′	117°18.0′	7 Sept. 1962	0142		55		Surface	Do.
94.30	C6208	144	32°39.0′	117°24.5′	32°38.0′	117°23.5′	4 Sept. 1962	2025	2131	275		183	Do.
94.32a	B6204	67	32°33.0′	117°27.5′	32°35.4′	117°30.8′	7 Apr. 1962	0218	0350	92	92	*37	Do.
94.32b	B6204	68	32°35.4′	117°30.8′	32°38.6′	117°33.3′	7 Apr. 1962	0400	0545	92	92	*37	Do.
95.30	C6208	145	32°37.0′	117°23.0′	32°35.0′	117°21.5′	4 Sept. 1962	2025	2131	275		Surface	Do.
95.31a	B6204	62	32°29.0′	117°21.5′	32°30.6′	117°23.1′	6 Apr. 1962	1320	1422	549–641	400	*282	Do.
95.31b	B6204	64	32°29.0′	117°21.6′	32°30.7′	117°24.5′	6–7 Apr. 1962	2305	0025	961	800	*563	Oblique.
95.31c	B6204	66	32°31.4′	117°21.6′	32°30.7′	117°24.5′	7 Apr. 1962	0043	0207	137	92	*37	Horizontal.
95.31d	B6204	69	32°30.7′	117°23.4′	32°32.2′	117°25.5′	7 Apr. 1962	1434	1625	686–1098	800	*563	Do.
97.40	C6303	197	31°49.0′	117°53.0′	31°45.2′	117°46.7′	21 Mar. 1963	1822	2115	421–439	732	*274	Oblique.
97.50	B6203	40	31°35.0′	118°30.7′			27 Mar. 1962	0140	0415	2,196	600	*423	Horizontal.
97.65	C6303	195	31°00.0′	119°32.0′	30°54.7′	119°28.4′	19 Mar. 1963	0858	1245	3,477	1,372	*458	Do.
99.31	C6208	138	31°54.4′	116°59.0′	31°51.5′	116°57.5′	1–2 Aug. 1962	2245	0020	732		66	Do.
100.40	H6204	70	31°21.2′	117°26.7′			12 Apr. 1962	0229	0414	1,874	800	*298	Do.
100 40	C6303	198	31°21.0′	117°27.0′	31°18.0′	117°27.3′	22 Mar. 1963	0450	0620	1,995	92	22	Do.
100.50	H6204	71	31°00.0′	118°09.9′			12 Apr. 1962	1020	1155	1,739	800	*298	Do.
100.60	H6204	72	30°39.0′	118°45.5′			12–13 Apr. 1962	2120	0205	2,782	4,530	*1,676	Do.
100.65	C6303	196	30°32.5′	119°09.8′	30°26.4′	119°06.2′	19 Mar. 1963	1530	1930	3,111	1,372	*458	Do.
100.80	H6204	73	29°58.5′	120°07.0′			13 Apr. 1962	1630	2100	3,962	4,530	*1,676	Do.
100.90	H6204	74	29°38.0′	120°46.8′			14 Apr. 1962	0048	0305	3,861	800	*298	Do.
100.100	H6204	75	29°19.0′	121°25.0′			14 Apr. 1962	0941	1347	3,843	4,530	*1,676	Do.
100.120	H6204	76	28°40.5′	122′46.8′			14 Apr. 1962	2230		4,099	800	*298	Do.
100.140	H6204	77	27°59.4′	124°05.8′			15 Apr. 1962	1008	1416	4,209	4,530	*1,676	Do.
100.160	H6204	78	27°22.6′	125°20.0′			6 Apr. 1962	0306	0724	4,145	4,530	*1,676	Do.
103.50	C6303	199	30°18.4′	117°47.0′	30′05.5°	117°45.2′	22 Mar. 1963	1300	1830	2,837	824	220	Do.
107.60	C6303	200	29°30.0′	118°00.0′	29°21.0′	118°00.0′	22–23 Mar. 1963	2230	0200	3,569	46	9	Do.
108.63	C6303	201	29°12.1′	118°09.0′	29°13.8′	118°03.5′	23 Mar. 1963	0328	0620	1,830	1,372	*458	Do.
110.35	H6204	84	29°46.5′	115°58.5′			21 Apr. 1962	0200	0400	1,153	800	*298	Do.
110.35	C6303	203	29°46.3′	116°01.2′	29°42.8′	115°59.0′	23 Mar. 1963	2100	2315	1,153	732	*201	Do.
110.36	C6303	204	29°41.2′	116°41.2′	29°36.2′	115°59.0′	24 Mar. 1963	1225	1624	1,830	1,190	*403	Do.
110.40	H6204	83	29°32.4′	116°15.1′			20 Apr. 1962	2120	2300	2,416	800	*298	Do.
110.46	C6303	202	29°28.4′	116°47.0′	29°25.8′	116°45.0′	23 Mar. 1963	1412	1600	1,830	640	*156	Do.
110.50	B6203	44	29°16.5′	116°59.0′			28 Mar. 1962	0100	0330	3,660	600	*423	Do.
110.100	H6204	82	27°32.1′	120°14.0′			19 Apr. 1962	0520	0700	3,953	800	*298	Do.
110.120	H6204	81	26°56.8′	121°32.4′			18 Apr. 1962	1644	2057	4,269	4,530	*1,676	Do.
110.140	H6204	80	26°16.0′	122°49.2′			18 Apr. 1962	0653	0750	4,108	1,100	*410	Do.
110.160	H6204	79	25°34.7′	124°07.0′			17 Apr. 1962	1530	1930	4,200	4,530	*1,676	Do.
111.36a	C6303	207	29°41.5′	115°59.6′	29°34.7′	115°57.5′	26 Mar. 1963	0200	0550	1,830	686	*165	Do.
111.36b	C6303	208	29°39.1′	116°01.3′	29°32.4′	116°00.6′	26 Mar. 1963	0900	1330	2,196			
111.37a	C6303	205	29°34.7′	116°00.0′	29°32.0′	115°59.0′	25 Mar. 1963	0912	1255	2,196	1,372	*366	Oblique.
111.37b	C6303	206	29°38.9′	116°01.8′	29°31.0′	116°00.4′	25 Mar. 1963	1425	1900	2,196	1,372	*403	Do.
113.34a	C6303	209	29°13.0′	115°30.7′	29°10.8′	115°28.5′	26 Mar. 1963	1700	1840	220	640	150	Horizontal.
113.34b	C6303	210	29°21.0′	115°38.0′	29°14.5′	115°32.4′	27 Mar. 1963	1040	1435	549	686	*192	Oblique.
118.43	B6212	152	28°11.0′	115°41.6′	28°08.0′	115°40.5′	1 Dec. 1962	1257	1434	586	657	*306	Horizontal.
120.45	H6204	85	27°43.2′	115°32.3′			22 Apr. 1962	1634	1813	3,294	800	*298	Do.
120.45	B6212	153	27°44.0′	115°33.0′	27°38.7′	115°30.2′	1 Dec. 1962	1724	1922	2,196	600	*311	Do.
120.50	H6204	86	27°29.1′	115°51.5′			22–23 Apr. 1962	2305	0328	3,916	4,530	*1,676	Do.
120.60	H6204	87	27°00.0′	116°36.3′			23 Apr. 1962	0850	1023	3,660	800	*298	Do.
120.70	H6204	88	26°51.0′	117°09.2′			23 Apr. 1962	1640	2042	3,660	4,530	*1,676	Do.
120.80	H6204	89	26°31.0′	117°47.0′			24 Apr. 1962	0044	0223	3,861	800	*298	Do.
120.90	H6204	90	26°09.0′	118°26.2′			24 Apr. 1962	0715	1135	4,063	4,530	*1,676	Do.
123.45	B6212	154	27°08.0′	115°11.4′	27°01.2′	115°09.4′	1–2 Dec. 1962	2312	0137	4,118	150	*55	Do.
123.50	B6203	47	26°58.0′	115°31.0′			28–29 Mar. 1962	2325	0225	3,660	600	*423	Do.
127.45	B6212	155	26°32.8′	114°54.0′	26°27.5′	114°50.7′	2 Dec. 1962	0520	0752	3,203	600	*320	Do.
130.40	B6212	156	26°12.0′	114°14.5′	26°07.0′	114°14.0′	2 Dec. 1962	1219	1433	2,745	800	*412	Oblique.
133.35	B6212	157	25°45.5′	113°27.0′	25°41.5′	113°31.0′	2 Dec. 1962	1952	2148	366	500	*240	Do.
137.35	B6212	158	25°06.0′	112°56.0′	25°01.0′	112°56.0′	3 Dec. 1962	0309	0510	1,281	400	*176	Do.
137.50	B6203	49	24°40.0′	114°02.0′			29–30 Mar. 1962	2152	0034	3,660	600	*423	Horizontal.
140.35	B6212	159	24°35.5′	112°42.5′	24°29.0′	112°42.0′	3 Dec. 1962	0803	1032	732	800	*426	Oblique.
143.30	B6212	160	24°11.0′	112°03.0′	24°08.0′	112°02.3′	3 Dec. 1962	1457	1612	176–183	390	*152	Do.
147.30	B6212	161	23°42.0′	111°44.0′	23°39.5′	111°36.0′	3 Dec. 1962	1925	2150	275	400	*176	Do.

Cruise B6212: R/V *Black Douglas;* December 1–3, 1962; central to southern Baja California, to about 80 km. (50 miles) seaward; 10 tows with CMWBT: 55–176 (4), 240–311 (3), 386–426 (3); other work, collections at Marquis Point and Magdalena and Santa Maria Bays, Baja California, using seines, rotenone, otter trawls, and dip nets.

Cruise B6303: R/V *Black Douglas;* February 28 to March 18, 1963; Point Conception to off San Diego, Calif., to about 480 km. (300 miles) seaward; 13 tows with CMWBT: 18–73 (3), 113–201 (3), 274–386 (5), unknown (2); negative tows, stations 87.70a, 87.70b; other work, oblique and horizontal tows with 1-m. standard plankton net and 1-m. closing net and bottom trawling with 16-ft. otter trawl.

Cruise C6303: R/V *John N. Cobb;* March 1–27, 1963; Point Conception, Calif. to central Baja California, to about 430 km. (270 miles) seaward; 36 tows with *Cobb* pelagic trawl Mark II: 9–27 (5), 82–192 (10), 201–403 (15), 458–489 (4), 640 (2); negative tows, stations 80.70, 85.68, 111.36b.

STATION DATA

The basic station numbering system in use since 1950 for the California Cooperative Oceanic Fisheries Investigations (CalCOFI) was used for station designation during the pelagic survey (fig. 1). An explanation of this numbering plan was

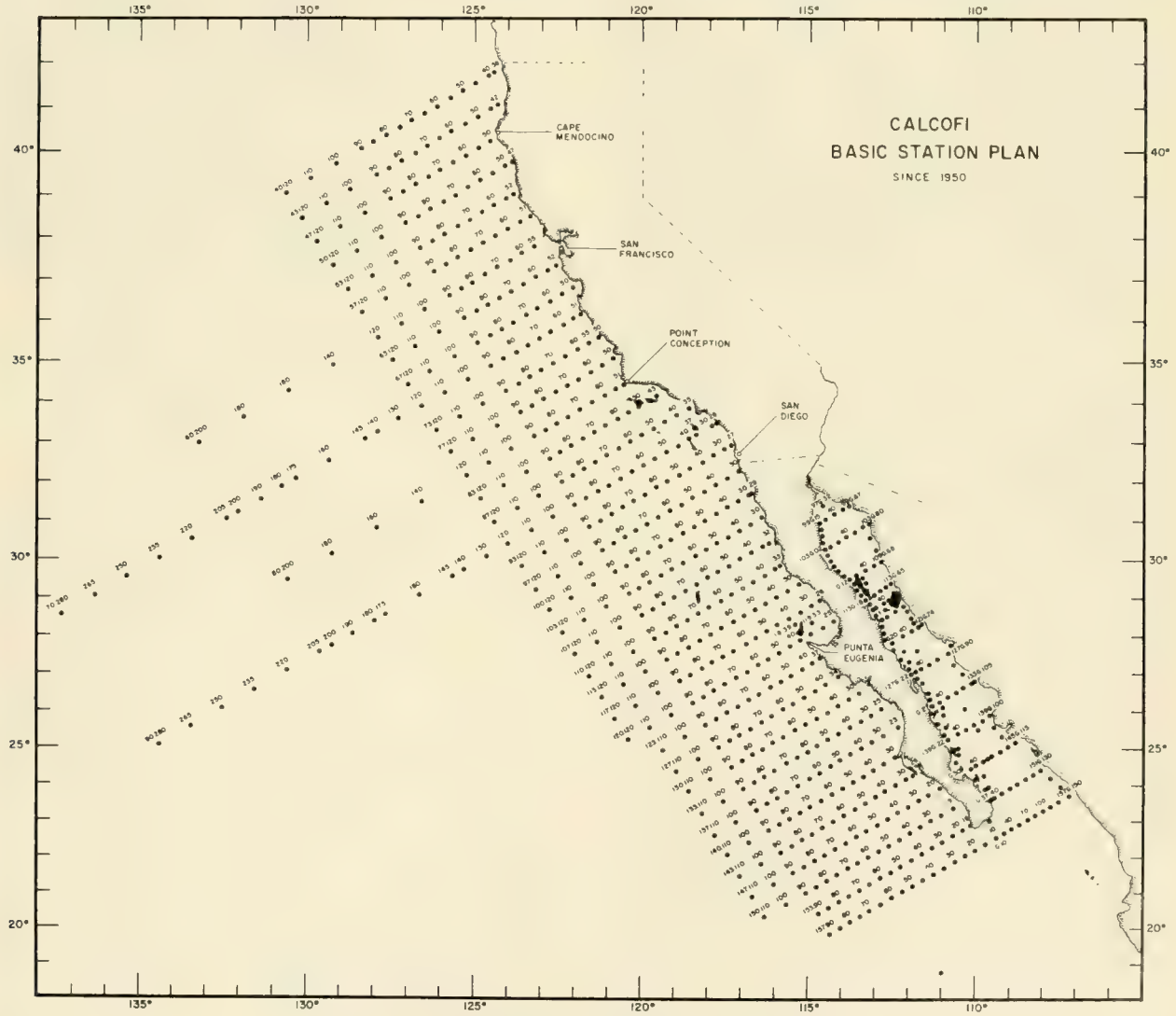


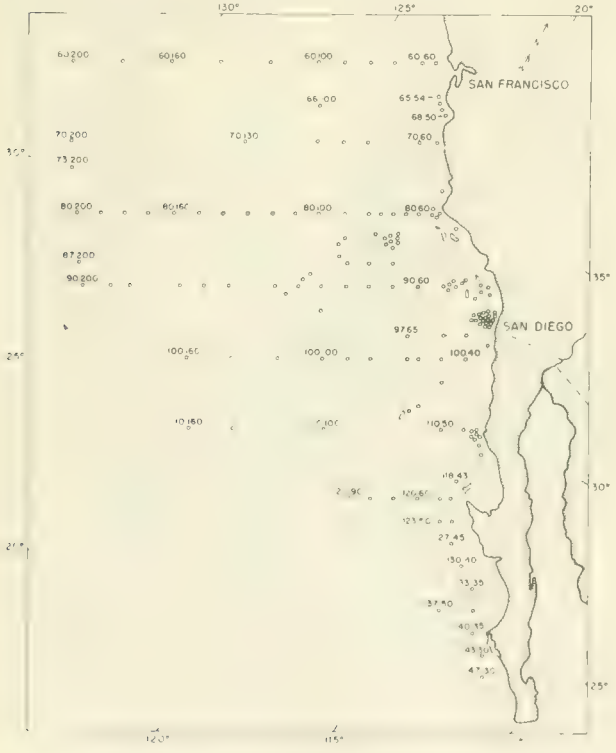
FIGURE 1.—CalCOFI basic station plan since 1950.

given by Scripps Institution of Oceanography and Fish and Wildlife Service (1952). The stations occupied during the eight cruises are shown in figures 2A and 2B.

The station data for the cruises are given in table 1. An asterisk in the table indicates an approximate value. The stations are listed in increasing numerical order by line from north to south and by station number from east to west. When the same station was occupied more than once during a cruise, the earliest occupancy was designated "a", the next "b", . . . The depth fished was determined or estimated in a variety of ways. A depth telemeter with a conducting cable was used for some stations on cruise C6208; the Brown Depth Recorder for several stations on cruises H6105 and H6204; and a bathykymograph for a few stations on cruises B6203, B6204, B6212, and B6303. For some stations on cruise H6204, a factor of 0.37 times the length of the wire out, was used to estimate the depth fished.

The depth of bottom at each station, the amount of wire out, and the depth fished are recorded in meters. This has produced some uneven or irregular numbers that are frequently repeated in table 1. One reason for this is that depth of bottom at each station was originally recorded in fathoms, either from the depth recorder or chart reading, and was subsequently converted to meters to conform to the required style of this report. At a number of stations on some of the cruises, the amount of wire out was set at a particular number of meters, and the calculated or estimated fishing depth was a reflection of amount of wire out (for example, on cruise H6204 most stations were made with either 800 or 4,500 m. of wire out, and the estimated depth of fishing was 298 and 1,676 m., respectively).

The types of tows are listed as horizontal or oblique. For horizontal tows, a selected amount of wire was let out and the trawl was towed within a generally restricted depth range. Obviously, the trawl was fishing in descent to and ascent from this depth, but most of the fishing effort for a horizontal tow was usually near the maximum depth fished. It is recognized that after the selected amount of wire has been let out, the trawl may sink for a time while being towed. Also, if



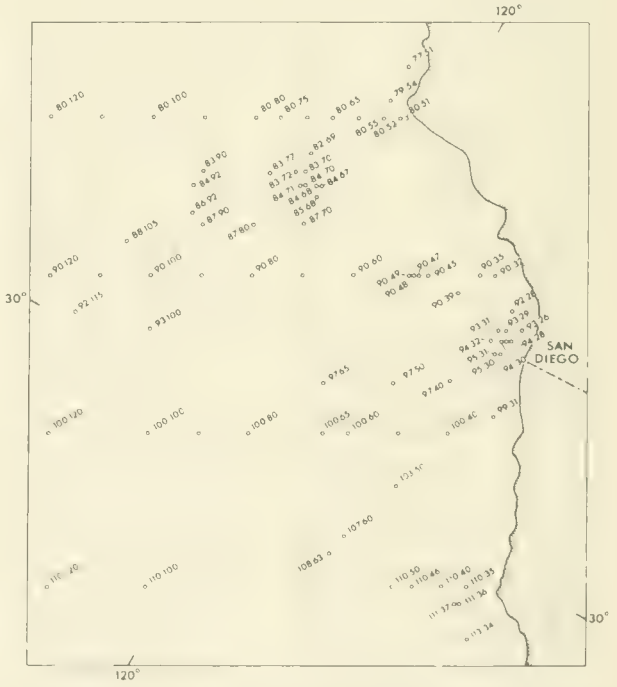


FIGURE 2. (A) Stations occupied during pelagic survey. (B) Stations occupied in the central and shoreward portion of the pelagic survey.

the ship's speed is reduced when the wire retrieval begins, the trawl may sink and continue fishing deeper than the calculated maximum depth recorded for the horizontal tow. The oblique tows were made in two ways: (1) by letting out a selected length of wire as fast as feasible and retrieving slowly or in stages (as, on a deep tow, taking in 100 m. of wire during about 3 to 5 minutes and towing for 10 minutes before retrieving more wire) and (2) by letting the wire out slowly or in stages and retrieving as fast as possible.

COLLAPSIBLE MIDWATER BEAM TRAWL

On vessels such as the *Black Douglas*, inadequately equipped to operate (most) large nets, it was necessary to have a collapsible net (fig. 3). Views of operation of the net and certain details of construction and the jury-rigged winch and H-frame aboard the *Black Douglas* are shown in figures 4 and 5.

In devising the CMWBT, several features desirable in operating such a net were considered, and attempts were made to incorporate these features into the design and function.

Mouth opening.—This should be large to sample a relatively large area and to reduce escapement. The horizontal opening was fixed at 10 feet by the top and bottom beams. The vertical, nonrigid opening was hung at 14 feet. In towing, the vertical opening was reduced to about 12 feet at 2 knots and to about 10 feet at 4 knots; the latter still left a sampling area of about 100 square feet.

Towing speed.—The CMWBT was strongly constructed. The maximum speed at which it was towed was about 5 knots, but faster speeds could have been used.

Mouth opening obstruction.—There was no obstruction from the top beam bridle, and that from the bottom beam bridle was not great; this could be eliminated by a spreader bar.

Specimen damage.—This was reduced by a specially constructed cod end (figs. 3 and 5D).

The bullet-shaped device attached to the top beam in figure 4 is a bathykymograph. This model functioned sporadically and unsatisfactorily in our experiments.

SUMMARY OF FISHES COLLECTED

More than 189 species of fishes were taken in the survey. The exact number cannot be determined at this time because of the uncertain identification of more than 18 forms. At least one previous-

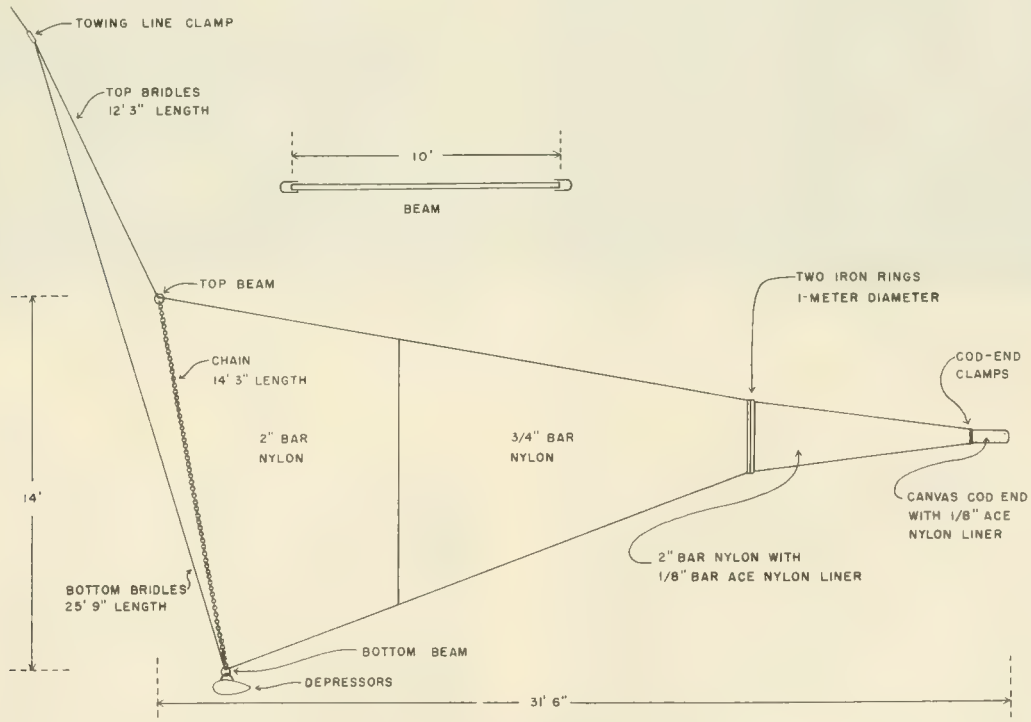


FIGURE 3.—Diagram (lateral view) of 10- by 14-ft. collapsible midwater beam trawl (CMWBT).

FIGURE 4.—CMWBT. A, emerging. B, boarding. C, top beam secured to H-frame, hauling in bottom beam. D, both beams secured. Cylinder attached to middle of top beam is bathykymograph.

ly unnamed and undescribed genus and at least four undescribed species were taken; these specimens have been made available to specialists working on the groups concerned. Sixteen orders of fish and 71 families are represented, including 52 species of the order Isospondyli, 51 species of Iniomi, and 37 of Percomorphi. The greatest number of species in a single family was 40 in the Myctophidae. The greatest number of species in a single genus was 12 in *Lampanyctus* (Myctophidae); the next greatest was 8 in *Melamphaes* (Melamphaidae).

About 52,000 fish were taken in the pelagic survey. The order Isospondyli comprised about 56 percent of this total, including the numerically most abundant species, *Engraulis mordax*, which itself was 34 percent of the total number. The Iniomi was the second most abundant order, about 38 percent of the total; the family Myctophidae comprised most of this percentage. The myctophid genus *Lampanyctus* (including the subgenus *Triphoturus*), was 21 percent of the total, and *Lampanyctus* (*Triphoturus*) *mexicanus* was the second most abundant species—about 18 percent

FIGURE 5.—CMWBT. A, towing; note H-frame, slush block, angle indicator, meter wheel, winch, and capstan. B, depressor and rib on back of bottom beam for lashing net. C, afterpart of net with two detachable one-meter rings. D, lined cod end and cod-end clamp.

of the total. Forty-four of the species were represented by a single specimen. The preponderance of anchovies (*Engraulis mordax*) in the above figures does not indicate a high relative abundance of this species over the survey area—as is true for *Lampanyctus* (*T.*) *mexicanus*—because the bulk of the anchovies taken on the survey was from two large catches at stations close to shore.

During the survey, 198 tows caught one or more fish (12 other tows did not catch fish, for various reasons). Species of Myctophidae were taken at more of the "successful stations" than any other family. *Lampanyctus* (*T.*) *mexicanus* was taken at 76 stations—more than any other species. Other myctophids caught at a relatively large number of stations were: *Heirops crockeri* and *Ceratoscopelus townsendi* (66 stations each), *Lampanyctus ritteri* (63 stations), *Diaphus theta* (61), *Symbolophorus californiense* (55), and *Stenobrachius leucopsarus* (54). Of the Gonostomatidae, *Cyclothone signata* was taken at 64 stations, *Cyclothone acclinidens* at 49, and *Danaphos oculatus* at 47.

Three species of Sternoptychidae were captured at a large number of stations—*Argyropelecus hawaiensis* at 54, *A. pacificus* at 49, and *A. intermedius* at 45. Three other species collected at a number of stations were *Idiacanthus antrostomus* and *Scopelogadus mizolepis bispinosus* (50 each) and *Merluccius productus* (42). Sixty of the species recorded were caught at only one station.

The most abundant species in a single tow was *Engraulis mordax*—about 9,000 specimens (450 pounds) taken at a single station. *Lampanyctus* (*T.*) *mexicanus* had the next highest numbers—about 3,000 specimens at one station and 1,857 at another. Other large single collections were *Ceratoscopelus townsendi* (944), *Stenobrachius leucopsarus* (735), *Vinciguerria lucetia* (537), *Merluccius productus* (495), and *Leuroglossus stilbius* (396).

The maximum number of species in a single tow was 44, with the *Cobb* pelagic trawl on cruise C6303 at station 86.92. On the same cruise, relatively large numbers of species per tow were taken at stations 100.65 (41 species), 83.77 (38), and 87.80 (37). Maximum numbers of species per tow with the 10-ft. Isaacs-Kidd midwater trawl (IKMWT) were taken on cruise H6204 at stations 80.90 (34 species) and 60.60 (32). The maximum number of species per tow with the collapsible net was 21 on cruise B6303 at station 84.92.

Many variables affected the numbers and species of fishes caught on the survey including depth of tow, time of year, diurnal migration, speed and length of tow, size of net, size of net webbing, and water mass sampled. Because of these variables, many of the numbers and percentages just cited relate to the survey rather than to the character of the pelagic environment.

For abundant and for more significant species, the locations of capture are shown on distribution charts. These charts bear one symbol for each station at which a species was caught—they do not indicate the capture of a species more than once at a single station.

The specimens preserved from the pelagic survey have been placed in four collections. Some of the larval and juvenile forms are in the Bureau of Commercial Fisheries California Current Resources Laboratory. A small representative series of the bathypelagic species is in the Stanford University Natural History Museum. A large representative series of most species taken is in the Fish Division of the U.S. National Museum. The remainder of the material, comprising the bulk of the collection and representatives of most species taken, is in the Marine Vertebrate Collection of Scripps Institution of Oceanography. The disposition of all the specimens is recorded in the Field Data Books of the Bureau Laboratory at La Jolla and in the collection records at Scripps Institution of Oceanography. Representative type material of any new taxa that are based on these specimens will be placed in the U.S. National Museum.

ANNOTATED LIST OF FISHES

In preparing the data for this report we attempted, with the help of other ichthyologists, to determine specific identifications of the specimens. Many taxonomic problems were not solved; we briefly describe these in the annotations of the species and also include our resolutions of some of the problems.

The fishes listed below are arranged phylogenetically by order and family. Each record of capture is listed under the species in the following abbreviated form, from left to right: the station of capture; the cruise during which the station was occupied; the number of specimens taken at that station, in parentheses; and the length or length range in millimeters of the specimens. For some collections, numbers or lengths of specimens are not available; for others, weight instead of length is given. At a few stations specimens were discarded at sea before accurate records were made.

Lengths of specimens are given in millimeters of standard length (SL), except where otherwise noted. Total length (TL) is used for a few species, and where this designation is given for the initial entry in a species list, all subsequent measurements in that list are in total length. Specimens 100 mm. in length and larger were measured to the nearest millimeter; most specimens smaller than 100 mm. were measured either to the nearest millimeter, or to the nearest half-millimeter. In collections with damaged specimens that were not measured, "dis." (disintegrated) is used instead of a length. A plus sign following the length measurement of some specimens indicates that a portion of the posterior end of the body was missing.

ELASMOBRANCHII

CARCHARHINIDAE

1. *Prionace glauca* (Linnaeus).
Figure 6A.

60.55, C6208, (4) 865–1,785 mm. TL; 65.54, C6208, (3) 1,255–1,365 mm.; 91.39b, C6208, (1) 568 mm.; 107.60, C6303, (1) 1,200 mm.

MYLIOBATIDAE

2. *Holorhinus californicus* (Gill).
Figure 6A.

93.26, C6208, (3) ca. 5 kg., no length recorded.

TORPEDINIDAE

3. *Torpedo californica* Ayres.
Figure 6A.

77.51, C6208, (1) 453 mm. TL; 80.52, C6208, (1) 422 mm.; 94.28b, C6208, (1) ca. 5 kg.; no length recorded.

This species is generally considered to be a benthic inhabitant of moderately deep water. For the first two records above, however, night tows of the *Cobb* pelagic trawl at the surface (trawl fishing no deeper than 24 m.) captured single specimens of *Torpedo* about 24 km. (15 miles) offshore in water about 350 to 690 m. deep.

ISOSPONDYLI

CLUPEIDAE

4. *Sardinops caerulea* (Girard).
Figure 6B.

94.28b, C6208, (9) 225–275 mm.; 94.29b, C6208, (43) 195–235 mm.; 84.29c, C6208, (2) 195 mm.; 94.30, C6208, (1) 225 mm.

ENGRAULIDAE

5. *Engraulis mordax* Girard.
Figures 6B and 7.

65.54, C6208, (ca. 450) 113–150 mm.; 66.50, C6208, (few) ca. 102 mm.; 70.60, C6208, (1) 33 mm.; 70.80, C6208, (2) 29–30 mm.; 70.90, C6208, (17) 21–27 mm.; 77.51, C6208, (ca. 250) 102–143 mm.; 80.52, C6208, (10) 28.5–143 mm.; 80.60, C6208, (1) 37 mm.; 80.65, B6303, (1) 121 mm.; 80.80, H6204, (1) 141 mm.; 82.45, C6208, "10 lbs. (4 kg.) in all," sample (19) 109–150 mm.; 82.69, C6303, (58) 118–144 mm.; 83.70b, B6303, (25) 120–140 mm.; 83.70c, B6303, (1) 131 mm.; 84.70, C6303, (44) 120–137 mm.; 87.90 C6303, (1) 150 mm.; 90.32, H6204, (3) 108–123 mm.; 90.45, H6105, (13) 4–14 mm.; 90.48b, H6105, (193) 4–28 mm.; 92.28, C6208, (50) ca. 125 mm.; 93.28, C6208, (ca. 100) 2 kg. adults; 93.29, C6208, (200 kg.) 100 fish sample, 85–135 mm.; 94.29b, C6208, (4) ca. 100 mm.; 94.29c, C6208, (16) 55–125 mm.; 95.30, C6208, (1) 150 mm.; 97.40, C6303, (1) 121 mm.; 99.31, C6208, (16) ca. 50 mm.; 107.60, C6303, (2) 123–126 mm.; 110.35, C6303, (6) 116–126 mm.; 113.34b, C6303, (ca. 170 kg.) 115–135 mm.; 120.45, H6204, (2) 16–17.5 mm.; 120.50, H6204, (2) 12.5–14 mm.

Anchovies were taken at 33 stations. Nine of these records were of larvae or small juveniles from close inshore to about 260 km. (160 miles) offshore. Three stations produced records of anchovies that add significantly to our knowledge of the biology of this species. (1) At station 89.90, C6303, one adult was taken about 400 km. (250 miles) from nearest landfall. (2) At station 83.70, B6303, in the San Juan Seamount area—where hake eggs were abundant in routine oblique plankton tows (to about 140 m.), and where freshly spent hake were caught in about 121 and 165 m.—anchovy eggs were abundant in a near-surface plankton tow (about 5.5 m.), and running ripe anchovies were caught in a midwater trawl at about 81 m. The *Cobb* echo sounder showed subsurface concentrations at 73 m. and 146 to 220 m. in this area. These concentrations probably represented anchovies spawning above a deeper school of hake that was spawning or had just finished spawning. (3) At station 93.29, C6208, 13 km. (8 miles) off La Jolla over water about 475 m. (260 fathoms) deep, the *Cobb* Simrad registered a dense concentration at about 201 m. (110 fathoms) (fig. 7). With the aid of the depth telemeter, the trawl was towed through this area. The resulting catch was 200 kg. of anchovies. The Simrad was monitored throughout the tow; and the lack of other concentrations indicated that a dense and unusually deep school of anchovies was sampled. A bathythermograph (BT) cast at this station showed a surface temperature of 68° F., a thermocline at about 18 to 82 m., and a temperature of 74° F. at 201 m.

ALEPOCEPHALIDAE

6. *Alepocephalus tenebrosus* Gilbert ?
Figure 6C.

80.90, H6204, (1) 12.5 mm.; 100.60, H6204, (1) 25 mm.; 100.80, H6204, (1) 28 mm.; badly damaged.

The specific identifications are questionable because of the small size of the specimens.

7. *Talismania bifurcata* (Parr).
Figure 6C.

90.120, H6204, (1) 33 mm.; 110.120, H6204, (1) 47 mm.; 120.50, H6204, (1) 44 mm.

SEARSIDAE

8. *Sagamichthys abei* Parr.
Figure 6C.

60.60, H6204, (2) 25.5–41.5 mm.; 60.80, H6204, (1) 45.5 mm.; 60.80, C6208, (2) 106–139 mm.; 60.90, H6204, (1)

FIGURE 6.—Locations of capture of: A, *Prionace glauca, Holorhinus californicus, Torpedo californica.* B, *Sardinops caerulea, Engraulis mordax.* C, *Alepocephalus tenebrosus?, Talismania bifurcata, Sagamichthys abei.* D, *Pellisolus facilis, Mirorictus taaningi, Holtbyrnia macrops?, Holtbyrnia* sp.

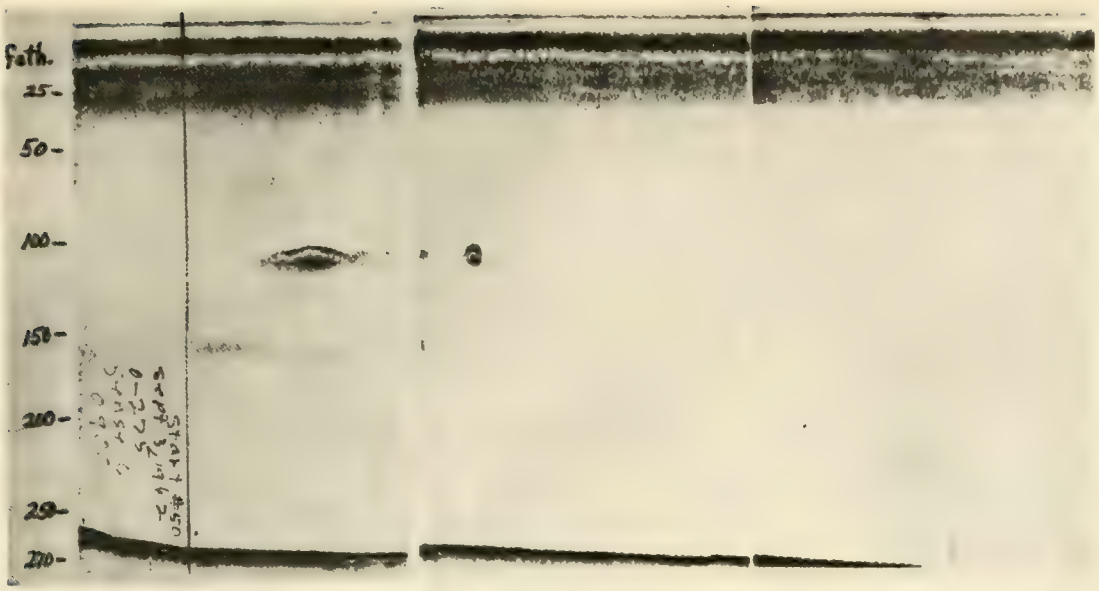


FIGURE 7.—Simrad tracing of a concentration 110 fathoms deep, presumed to be a school of *Engraulis mordax*. The recording, from left to right, is nearly continuous—the two vertical white lines were caused by brief intervals when the machine was not inking the paper. The vertical black line on the left is the reference mark indicating start of the tow at depth. *John N. Cobb* station 93.29, cruise C6208.

77 mm.; 60.100, H6204, (1) 24.5 mm.; 80.55, H6204, (1) 63 mm.; 80.70, H6204, (1) 21 mm.; 83.77, C6303, (4) 53.5–116 mm.; 86.92, C6303, (3) 106–215 mm.; 87.80, C6303, (3) 96–147 mm.; 90.48a, H6105, (5) 26–28.5 mm.; 90.70, H6204, (1) 38.5 mm.; 90.70, C6208, (2) 164–171 mm.; 95.31c, B6204, (4) 18–36.5 mm.; 97.50, B6203, (1) 35.5 mm.; 97.65, C6303, (8) 43–223 mm.; 100.40, H6204, (1) 37 mm.; 100.60, H6204, (1) 118 mm.; 100.65, C6303, (28) 63–252 mm.; 100.90, H6204, (1) 90 mm.; 100.100, H6204, (1) 121 mm.; 108.63, C6303, (52) 128–245 mm.; 120.80, H6204, (1) 58.5 mm.; 140.35, B6212, (1) ca. 18 mm.

These specimens differ in certain respects from the original description of the holotype by Parr (1960: 42), but further study is necessary to evaluate these differences (R. J. Lavenberg, personal communciation). The *Cobb* Mark–II pelagic trawl took this species in relatively large numbers (52 in one tow and 28 in another) and at larger sizes (up to 252 mm.) than were previously recorded.

9. *Pellisolus facilis* Parr.

Figure 6D.

90.120, H6204 (1) 56.5 mm.

This specimen represents an appreciable range extension from the type locality south of Panama given by Parr (1960: 97).

10. *Mirorictus taaningi* Parr.

Figure 6D.

120.70, H6204, (1) 120 mm.

The jaw morphology and mechanism in this and another specimen examined are like that of all other alepocephalids and most other fishes and not like that described for the apparently distorted holotype by Parr (1960: 30). This fish and a specimen in the collection of Scripps Institution of Oceanography from near Guadalupe Island extend the recorded range of the species from the type locality in the Gulf of Panama.

11. *Holtbyrnia macrops* Maul?

Figure 6D.

80.90, H6204, (2) 23–64 mm.; 100.140, H6204, (1) 33 mm.

These specimens are questionably identified, because slight differences suggest that they may be specifically distinct from the species described from off Madeira by Maul (1957: 11) (R. J. Lavenberg, personal communication). This species was placed in a new subgenus, *Krefftia*, by Parr (1960: 71).

12. *Holtbyrnia* sp.

Figure 6D.

80.100, H6204, (1) 22.5 mm.; 90.45a, H6105, (2) 28–29.5 mm.; 90.48a, H6105, (9) 15–33.5 mm.; 120.90, H6204, (1) 31.5 mm.

These specimens are specifically distinct from those listed above as *Holtbyrnia macrops* Maul ? and may represent an undescribed species (R. J. Lavenberg, personal communication).

ARGENTINIDAE

13. *Nansenia* sp.

90.120, H6204, (1) 10.5 mm.

This specimen was taken about 500 km., southeast of Point Conception, Calif. There appear to be two species of *Nansenia* in the eastern North Pacific—a more northern form described as *N. candida* by Cohen (1958: 53) and a more southern form which is apparently undescribed. The above specimen, because of its small size and the intermediate location of its capture between the known ranges of the two species, cannot now be specifically identified (E. H. Ahlstrom, personal communication). The familial classification of this and the six following genera of argentinoid fishes was proposed by D. M. Cohen (personal communication).

14. *Argentina sialis* Gilbert.

95.31b, B6204, (1) 22.5 mm.

This specimen was taken about 25 km. (15 miles) west of San Diego, Calif.

15. *Microstoma microstoma* (Risso).

83.90, C6303, (1) 115 mm.

This specimen was taken about 275 km. (170 miles) southeast of Point Conception, Calif.

BATHYLAGIDAE

16. *Leuroglossus stilbius* Gilbert.

Figure 8A.

70.80–5N, B6203, (1) 31 mm.; 77.51, C6208, (1) 89 mm.; 80.55, H6204, (5) 33.5–107 mm.; 80.60, H6204, (1) 46 mm.; 80.70, H6204, (1) 32 mm.; 80.90–5N, B6203, (4) 28.5–32 mm.; 80.90, H6204, (3) 30.5–69 mm.; 82.45, C6208, (123) 47–94 mm.; 82.69, C6303, (39) 28–109 mm.; 83.70c, B6303, (2) 61.5–74 mm.; 83.70, C6303, (3) 78–90 mm.; 84.70, C6303, (28) 61–110 mm.; 90.32, H6204, (52) 32–99 mm.; 90.45a, H6105, (99) 22–106 mm.; 90.48a, H6105, (339) 5.5–51 mm.; 90.48b, H6105, (396) 5–23 mm.; 90.48c, H6105, (2) 22–25 mm.; 90.60, H6204, (10) 31–74.5 mm.; 90.70, C6208, (1) 28 mm.; 94.32a, B6204, (19) 29.5–55 mm.; 94.32b, B6204, (25) 25.5–54.5 mm.; 95.31a, B6204, (2) 33–34.5 mm.; 95.31b, B6204, (14) 32.5–47 mm.; 95.31c, B6204, (18) 31.5–41 mm.; 97.40, C6303, (239) 35–105 mm.; 100.40, H6204, (1) mm.; 100.40, C6303, (1) 92.5 mm.; 100.65, C6303, (1) 18 mm.; 110.35, C6303, (338) 35–109 mm.; 111.36a, C6303, (ca. 50) adults damaged and discarded at sea; 120.45, H6204, (3) 26.5–44 mm.; 123.45, B6212, (1) 23.5 mm.; 133.35, B6212, (4) 33–40 mm.; 140.35, B6212, (1) 28 mm.

17. *Bathylagus ochotensis* Schmidt.

Figures 8A and 9.

60.60, H6204, (3) 18.5–25 mm.; 60.70, H6204, (1) 13.5 mm.; 60.80, H6204, (4) 18–22 mm.; 60.80, C6208, (1) 37.5 mm.; 60.90, H6204, (4) 24–30 mm.; 60.100, H6204, (3) 17–24 mm.; 60.140, H6204, (1) 23 mm.; 70.80b, B6203, (3) 18–22 mm.; 70.80–5N, B6203, (1) 21 mm.; 80.60, H6204, (2) 49–65 mm.; 80.70, H6204, (1) 25 mm.; 80.90–5N, B6203, (12) 48–80 mm.; 80.100, B6203, (1) 77 mm.; 83.69, C6303, (6) 75.5–119 mm.; 84.70, C6303, (2) 64–86 mm.; 86.92, C6303, (1) 55.5 mm.; 90.70, H6204, (1) 29 mm.; 108.63, C6303, (2) 56–66 mm.

This and the other three species of *Bathylagus* captured were identified with a key prepared by D.M. Cohen.

18. *Bathylagus wesethi* Bolin.

Figures 8B and 10.

60.60, H6204, (2) 68–72 mm.; 60.90, H6204, (6) 22–33.5 mm.; 60.100, H6204, (3) 23.5–46 mm.; 60.120, B6203, (3) 36.5–70 mm.; 60.140, H6204, (3) 28.5–38 mm.; 60.160, B6203, (1) 27 mm.; 60.180, H6204, (1) 25.5 mm.; 80.55, H6204, (6) 28.5–33 mm.; 80.60, B6203, (1) 60.5 mm.; 80.70, B6203, (1) 28 mm.; 80.70, H6204, (3) 33–34 mm.; 80.90–5N, B6203, (9) 32–52 mm.; 80.90, H6204, (11) 23.5–78 mm.; 80.100, H6204, (3) all ca. 27 mm.; 82.69, C6303, (12) 25–69 mm.; 83.70a, B6303, (1) 28 mm.; 86.92, C6303, (2) 39.5–47 mm.; 87.80, C6303, (3) 26.5–83.5 mm.; 90.45a, H6105, (22) 38–75 mm.; 90.60, H6204, (1) 27 mm.; 90.70, H6204, (3) 23–75 mm.; 90.120, H6204, (2) 17–23 mm.; 97.40, C6303, (71) 26.5–89 mm.; 97.50, B6203, (2) 29.5–33 mm.; 100.40, H6204, (5) 28.5–42 mm.; 100.60, H6204, (2) 22.5–25 mm.; 100.65, C6303, (14) 27.5–84 mm.; 100.80, H6204, (3) 21–82.5 mm.; 108.63, C6303, (98) 25–86 mm.; 110.46, C6303, (1) 30 mm.; 110.50, B6203, (27) 23–41.5 mm.; 120.45, H6204, (4) 27–48.5 mm.; 120.50, H6204, (5) 32–42.5 mm.; 120.80, H6204, (1) 44 mm.; 120.90, H6204, (1) 21.5 mm.; 123.45, B6212, (22) 22–42 mm.; 123.50, B6203, (1) 26.5 mm.

19. *Bathylagus pacificus* Gilbert.

Figure 8B.

60.60, H6204, (4) 31–65.5 mm.; 60.80, H6204, (2) 30–51 mm.; 60.100, H6204, (3) 57–92 mm.; 80.90, H6204, (3) 42.5–149 mm.; 90.48a, H6105, (1) 127 mm.

20. *Bathylagus milleri* Jordan and Gilbert.

Figure 8B.

60.80, C6208, (5) 86–128 mm.; 60.120, H6204, (2) 37.5–45.5 mm.; 86.92, C6303, (10) 126–179 mm.; 87.80, C6303, (5) 128–163 mm.; 90.70, C6208, (6) 128–170 mm.

FIGURE 8.—Locations of capture of: A, *Leuroglossus stilbius, Bathylagus ochotensis.* B. *Bathylagus wesethi, Bathylagus pacificus, Bathylagus milleri.* C, *Macropinna microstoma, Dolichopteryx longipes.* D, *Argyropelecus pacificus, Argyropelecus intermedius, Sternoptyx diaphana.*

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FIGURE 9.—*Bathylagus ochotensis*, juvenile, 25.5 mm. SL, station 73.50, H5204.

FIGURE 10.—*Bathylagus wesethi*, juvenile, 27 mm. SL, station 92.117, S4903.

This species has at times been referred to by its junior synonyms, *B. alascanus* Chapman and *B. arae* Schmidt (D. M. Cohen, personal communication).

OPISTHOPROCTIDAE

21. *Macropinna microstoma* Chapman.

Figure 8C.

60.70, H6204, (2) 18.5–20.5 mm.; 60.90, H6204, (1) 20.5 mm.; 83.77, C6303, (1) 31 mm.; 86.92, C6303, (11) 89–127 mm.; 87.80, C6303, (2) 120–133 mm.; 100.65, C6303, (1) 24.5 mm.

Previous collections in the eastern North Pacific had indicated this to be a rare and solitary species that did not attain a large size—no more than two specimens had been taken together in the same net, and the largest size reported was 40.7 mm. (Bradbury and Cohen, 1958:59). The large *Cobb* Mark–II pelagic trawl caught 11 specimens up to 133 mm. SL in one tow; such large nets clearly sample the bathypelagic zone more adequately. The 13 larger specimens (89–133 mm.) all appeared sexually mature; the females had large ovarian eggs.

The ovarian eggs showed the following (John S. MacGregor, personal communication). The largest developing eggs had diameters of 2.17 to 2.53 mm.—a 95-mm. SL female had 497 eggs. The largest remnant egg was 3.47 mm. in diameter and had a 0.91-mm. oil drop in a 123-mm. SL female that also contained 669 developing eggs of 0.76 to 1.01 mm. diameter.

22. *Dolichopteryx longipes* (Vaillant).

Figure 8C.

83.90, C6303, (1) 74 mm.; 97.65, C6303, (1) 138 mm.; 108.63, C6303, (4) 51–180 mm.; 110.140, H6204, (1) 53.5 mm.

These specimens were identified with a key prepared by D. M. Cohen.

STERNOPTYCHIDAE

23. *Argyropelecus pacificus* Schultz.

Figure 8D.

60.60, H6204, (2) 25–42 mm.; 60.70, H6204, (1) 30.5 mm.; 60.70, C6208, (1) 15.5 mm.; 60.90, C6208, (1) 56.5 mm.; 60.160, B6203, (2) 62.5–69.5 mm.; 80.55, H6204, (2) 17–18.5 mm.; 80.60, H6204, (6) 15–52.5 mm.; 80.60, C6208, (8) 42–58 mm.; 80.70, H6204, (1) 19 mm.; 80.70, C6208, (2) 47.5–54 mm.; 80.90, H6204, (2) 16.5–39 mm.; 83.74, C6303, (105) 17–80 mm.; 83.90, C6303, (62) 19.5–63 mm.; 84.67, C6303, (9) 18–27.5 mm.; 84.70, C6303, (1) 50 mm.; 86.92, C6303, (5) 19–68 mm.; 87.80, C6303, (3) 27–78.5 mm.; 90.45a, H6105, (1) 48 mm.; 90.45, H6204, (2) 18.5–19 mm.; 90.47, C6208, (37) 18–54 mm.; 90.48a, H6105, (1) 24.5 mm.; 90.60, C6208, (5) 50–59.5 mm.; 90.70, H6204,

(2) 21–45 mm.; 90.70, C6208, (11) 40–62 mm.; 90.120, H6204, (4) 12–37 mm.; 90.140, H6204, (1) 55 mm.; 94.32b, B6204, (2) 17–18 mm.; 97.40, C6303, (17) 36–73 mm.; 97.50, B6203, (2) 45–50 mm.; 97.65, C6303, (39) 22.5–68.5 mm.; 100.40, H6204, (2) 22–35.5 mm.; 100.60, H6204, (11) 24.5–66.5 mm.; 100.65, C6303, (45) 24–67 mm.; 100.90, H6204, (1) 55 mm.; 100.160, H6204, (1) 66.5 mm.; 108.63, C6303, (195) 13–69 mm.; 110.35, C6303, (1) 58 mm.; 110.46, C6303, (40) 21–67.5 mm.; 110.120, H6204, (3) 38–62 mm.; 111.36a, C6303, (ca. 30) adults and juveniles damaged and discarded at sea; 111.37b, C6303, (71) 21–70 mm.; 120.45, H6204, (1) 26 mm.; 120.50, H6204, (3) 15.5–45.5 mm.; 120.70, H6204, (9) 22–56.5 mm.; 120.80, H6204, (3) 51.5–59 mm.; 120.90, H6204, (5) 23.5–50.5 mm.; 123.50, B6203, (5) 15.5–49 mm.; 130.40, B6212, (12) 30.5–55.5 mm.; 140.35, B6212, (8) 21.5–52 mm.

24. *Argyropelecus intermedius* Clarke.

Figure 8D.

60.70, H6204, (17) 9.5–23.5 mm.; 60.80, H6204, (2) 23–27 mm.; 60.90, H6204, (34) 12–34 mm.; 60.90, C6208, (2) 15.5–18 mm.; 60.100, H6204, (3) 14–25 mm.; 60.100, C6208, (2) 18.5–19 mm.; 60.120, B6203, (3) 23–24.5 mm.; 60.120, H6204, (8) 24–34 mm.; 60.140, H6204, (1) 26.5 mm.; 60.160, B6203, (1) 33 mm.; 60.160, H6204, (1) 33 mm.; 70.60, C6208, (1) 12.5 mm.; 80.55, H6204, (2) 16–19 mm.; 80.70, H6204, (1) 16.5 mm.; 80.80, H6204, (4) 22–25 mm.; 80.90, H6204, (4) 12–26 mm.; 80.140, C6208, (5) 18.5–33 mm.; 83.77, C6303, (8) 13.5–24 mm.; 83.90, C6303, (9) 18.5–31.5 mm.; 84.68, C6303, (1) 20 mm.; 84.92, B6303, (8) 20–28 mm.; 84.70, C6303, (1) 22 mm.; 86.92, C6303, (2) 20.5–23.5 mm.; 87.80, C6303, (1) 23 mm.; 87.90, C6303, (1) 24 mm.; 88.105a, B6303, (8) 18–23 mm.; 90.60, C6208, (2) 16.5–19 mm.; 90.70, H6204, (1) 19 mm.; 90.70 C6208, (2) 17 mm.; 90.100, C6208, (15) 15–31.5 mm.; 90.120, H6204, (1) 14 mm.; 90.140, H6204, (1) 28.5 mm.; 90.150, C6208, (1) 21 mm.; 90.200, C6208, (1) 28 mm.; 100.60, H6204, (1) 15 mm.; 100.65, C6303, (3) 21.5–29 mm.; 100.80, H6204, (3) 19.5–28 mm.; 100.90, H6204, (4) 23.5–28.5 mm.; 100.120, H6204, (3) 24–26 mm.; 100.140, H6204, (2) 18.5–26.5 mm.; 110.120, H6204, (1) 20 mm.; 110.140, H6204, (1) 23.5 mm.; 110.160, H6204, (3) 11–26 mm.; 120.80, H6204, (9) 13.5–23.5 mm.; 120.90, H6204, (1) 15 mm.

25. *Argyropelecus lychnus* Garman.

Figures 11 and 13A.

87.80, C6303, (1) 25 mm.; 90.45, H6204, (2) 15–17.5 mm.; 90.47, C6208, (1) 32 mm.; 90.48a, H6105, (2) 17.5–19.5 mm.; 90.120, H6204, (1) 12 mm.; 94.29a, C6208, (2) 30–30.5 mm.; 97.40, C6303, (4) 14–15.5 mm.; 97.50, B6203, (2) 21–39 mm.; 100.60, H6204, (2) 12–46 mm.; 100.90, H6204, (1) 48 mm.; 108.63, C6303, (2) 49–71.5 mm.; 110.35, C6303, (1) 17 mm.; 110.140, H6204, (1) 17.5 mm.; 120.45, H6204, (9) 14.5–27 mm.; 120.60, H6204, (2) 15.5 mm.; 120.80, H6204, (18) 20–61 mm.; 123.50, B6203, (6) 18–44 mm.; 130.40, B6212, (30) 17–58.5 mm.; 133.35, B6212, (1) 24.5 mm.; 137.50, B6203, (8) 19–43.5 mm.; 140.35, B6212, (3) 31–39 mm.

26. *Argyropelecus hawaiensis* Schultz.

Figures 12 and 13A.

60.60, H6204, (1) 12.5 mm.; 60.70, H6204, (3) 11–14.5 mm.; 60.80, H6204, (1) 16 mm.; 60.80, C6208, (2) 27–29 mm.; 60.90, H6204, (1) 13 mm.; 60.90, C6208, (2) 23–27 mm.; 60.100, H6204, (1) 30.5 mm.; 60.100, C6208, (4)

FIGURE 11.—*Argyropelecus lychnus*, juvenile, 17 mm. SL, station 110.140, H6204.

20.5–56 mm.; 60.120, B6203, (4) 36–39 mm.; 60.120, H6204, (1) 43 mm.; 60.140, H6204, (1) 37 mm.; 60.160, B6303, (2) 39.5–44 mm.; 60.160, H6204, (3) 15–51 mm.; 60.200, H6204, (2) 48–53 mm.; 70.60, C6208, (2) 20 mm.; 70.80b, B6203, (2) 14–38 mm.; 70.100, C6208, (1) 38 mm.; 80.55, H6204, (1) 37 mm.; 80.60, C6208, (5) 14.5–21 mm.; 80.70, C6208, (3) 18.5–19.5 mm.; 80.80, H6204, (4) 24–43 mm.; 80.90, B6203, (2) 18.5–44.5 mm.; 80.100, B6203, (5) 36–50 mm.; 80.140, C6208, (2) 44–56 mm.; 80.150, C6208, (1) 50.5 mm.; 83.70c, B6303, (1) 39.5 mm.; 83.77, C6303, (18) 23–40.5 mm.; 83.90, C6303, (16) 18–47.5 mm.; 84.67, C6303, (9) 16–35.5 mm.; 84.68, C6303, (3) 20–35 mm.; 84.70, C6303, (6) 20–37.5 mm.; 84.92, B6303, (9) 19.5–45.5 mm.; 86.92, C6303, (5) 37–43 mm.; 87.80, C6303, (1) 28 mm.; 90.32, B6203, (3) 16–18 mm.; 90.45, H6204, (1) 15.5 mm.; 90.47, C6208, (1) 46.5 mm.; 90.60, C6208, (1) 49.5 mm.; 90.180, C6208, (1) 58 mm.; 93.31, C6303, (4) 25–39 mm.; 94.29a, C6208, (3) 28–29.5 mm.; 97.40, C6303, (17) 18–43.5 mm.; 97.50, B6203, (1) 26.5 mm.; 97.65, C6303, (4) 30.5–43 mm.; 100.40, H6204, (1) 21.5 mm.; 100.40, C6303, (1) 40 mm.; 100.60, H6204, (2) 14.5–39 mm.; 100.65, C6303, (5) 33–43.5 mm.; 100.80, H6204, (1) 20 mm.; 100.90, H6204, (1) 35.5 mm.; 100.120, H6204, (1) 62 mm.; 103.50, C6303, (1) 22 mm.; 108.63, C6303, (2) 25–28 mm.; 110.46, C6303, (1) 26.5 mm.; 110.50, B6203, (2) 23–47.5 mm.; 120.60, H6204, (2) 16–53 mm.; 123.50, B6203, (4) 19.5–60.5 mm.

Argyropelecus hawaiensis was first described as a subspecies of *Argyropelecus lychnus* by Schultz (1961:615). With uncertainty, prompted by the small number of available specimens, Schultz recognized a complex of three subspecies:

A. l. lychnus Garman, eastern Pacific and Atlantic;

A. l. hawaiensis Schultz, around and north of Hawaiian Islands;

A. l. sladeni Regan, western Pacific and Indian Oceans.

In none of our specimens of this type is the body depth of as great a percentage of standard length as that given for *A. sladeni* by Schultz (1961 and 1937:4), and we do not consider *A. sladeni*, if valid, to occur within our area of study.

We conclude that *A. hawaiensis* is a species distinct from *A. lychnus*. In our study area *A. hawaiensis* has the more temperate distribution, and *A. lychnus*, the more subtropical (fig. 13A); but both species, often represented by specimens of similar size, were taken together at 11 stations of the survey. With a comparable size series of juvenile and adult specimens of about 12 to 62 mm. SL, certain character differences readily distinguish the two species.

The upper preopercular spine in juvenile *A. hawaiensis* curves outward and slightly dorsoposteriad in a nearly even arch, while in juvenile *A. lychnus* it curves outward and slightly ventroposteriad at its distal end. With increased body length this spine becomes relatively shorter and thicker in both species, but more strongly hooked upward in *A. hawaiensis* and more strongly hooked downward and backward in *A. lychnus*.

Juvenile specimens of *A. hawaiensis* possess considerably more lateral pigment along the posterior portion of the body (fig. 12). At about 14

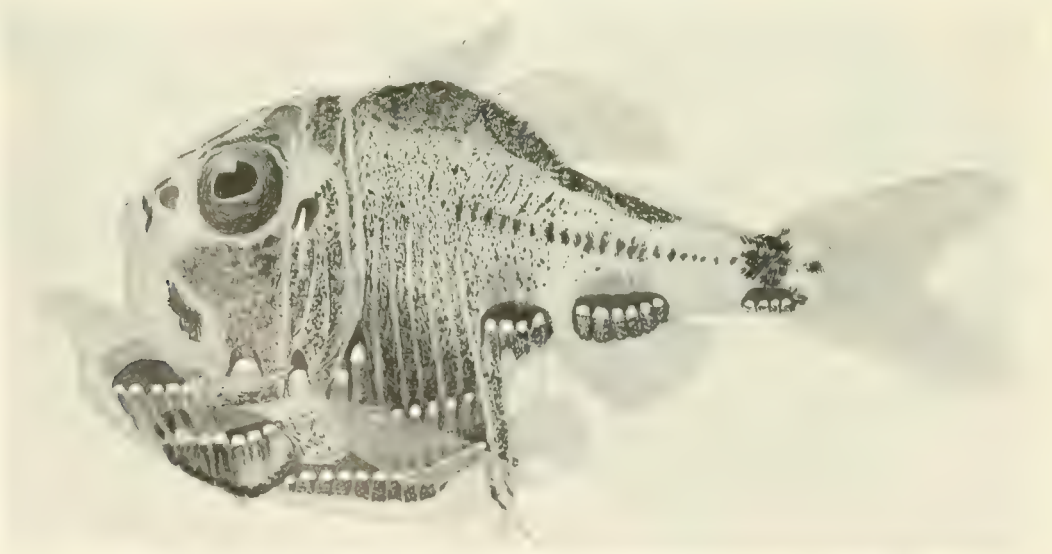

FIGURE 12.—*Argyropelecus hawaiensis*, juvenile, 17 mm. SL, station 84.67, C6303.

mm. SL, *A. hawaiensis* has a vertical band of pigment above the subcaudal photophores, a medial patch over the anal photophores, and a row of pigment spots along the lateral midline anterior to the anal photophores Specimens of *A. lychnus* of the same size possess no pigment on the posterior portion of the body, and pigment in the areas above the subcaudal and anal photophores begins to show only faintly at about 17 mm.

At about 25 mm. SL, body pigment extends backward to the posterior edge of the anal group of photophores on both species. The vertical area between the anal and subcaudal photophores in *A. hawaiensis* bears a row of pigment spots along the lateral midline (a posterior extension of the anterior row mentioned for the 14-mm. size). The area above the subcaudal photophores is strongly pigmented on both species and gives, on gross examination, the impression of a colorless, vertical band between the anal and subcaudal groups of photophores. This "banded" area fills in with pigment dorsoventrally in adults, and in 25-mm. specimens of *A. hawaiensis* the beginning of this process is evident. Specimens of the same size of *A. lychnus* have little or no pigment in this area, and the lower portion of this area immediately between the anal and subcaudal photophores may be void of pigment in specimens of *A. lychnus* as large as 42 mm. SL.

Body depth in relation to standard length overlaps between the two species in the smaller juvenile sizes. At larger sizes *A. lychnus* has the deeper body; above 32 mm. SL the body depth of *A. lychnus* is about 62–71 percent SL and that of *A. hawaiensis* about 54–60 percent SL.

An additional character useful in separating the two forms at sizes of about 45 mm. SL and larger is the formation of small spines along the ventral edges of the scales overlying the subcaudal photophores on specimens of *A. lychnus*. The spines start to develop on specimens between 40 and 45 mm. SL. These spines are absent on all specimens of *A. hawaiensis* examined including the largest in our collections (62 mm. SL) and one of the paratypes at Scripps Institution of Oceanography (SIO H53–372, 52 mm.).

27. *Argyropelecus* sp.

110.50, B6203, (1) 15 mm.

This damaged specimen cannot be specifically identified.

28. *Sternoptyx diaphana* Hermann.

Figure 8D.

60.80, H6204, (1) 43 mm.; 60.100, H6204, (3) 13–18.5 mm.; 60.180, H6204, (5) 8–29 mm.; 70.200, H6204, (6) 11–37 mm.; 80.70, H6204, (2) 14.5–16 mm.; 80.100, H6204, (1) 34 mm.; 83.77, C6303, (1) 25 mm.; 84.67, C6303, (1) 22.5 mm.; 86.92, C6303, (13) 14.5–57 mm.; 87.80, C6303, (3) 19–59 mm.; 87.90, C6303, (1) 54 mm.; 90.45a, H6105, (2) 24–37 mm.; 90.48a, H6105, (1) 27 mm.; 90.160, H6204, (5) 24–42.5 mm.; 90.180, H6204, (1) 19.5 mm.; 90.200, H6204, (4) 7–27.5 mm.; 95.31a, B6204, (1) 15 mm.; 100.65, C6303, (1) 28 mm.; 100.80, H6204, (4) 15–37 mm.; 100.140, H6204, (3) 28.5–36.5 mm.; 100.160, H6204, (3) 13–28.5 mm.; 110.120, H6204, (3) 32–39.5 mm.; 110.160, H6204, (10) 12.5–51 mm.; 120.45, H6204, (1) 32.5 mm.; 120.50, H6204, (1) 26.5 mm.; 120.90, H6204, (1) 31 mm.

GONOSTOMATIDAE

29. *Gonostoma atlanticum* Norman?

Figure 13B.

80.55, H6204, (1) 65 mm.; 80.80, H6204, (1) 45 mm.; 80.90, H6204, (1) 56 mm.; 90.100, C6208, (1) 28.5 mm.; 97.65, C6303, (1) 52 mm.; 100.120, H6204, (1) 63.5 mm.

These specimens appear to represent *G. atlanticum* Norman, but are only tentatively identified because of the arrangement of the maxillary teeth. Grey (1960:107) described the last four enlarged maxillary teeth of *G. atlanticum* as having no interspace teeth. The above specimens possess interspace teeth between the enlarged teeth on the maxillary.

30. *Gonostoma ebelingi* Grey.

Figure 13B.

90.160, C6208, (1) 124 mm.

This specimen represents an appreciable range extension from the original area of its description, the Marshall Island area, by Grey (1960:109).

31. *Cyclothone* Goode and Bean.

This is probably the most abundant deepwater genus of fishes off the coast of California. However, the collection data indicate that hauls made shallower than 550 m. do not adequately sample their population. Of the several thousand specimens taken by the IKMWT (the most efficient device in present use for the consistent capture of these fishes), only about 11 percent were taken where the net was fishing above an estimated depth of 550 m., and nearly all of these fish were *C. signata* and *C. acclinidens*—apparently the two most abundant species in the California-Baja California area at any depth.

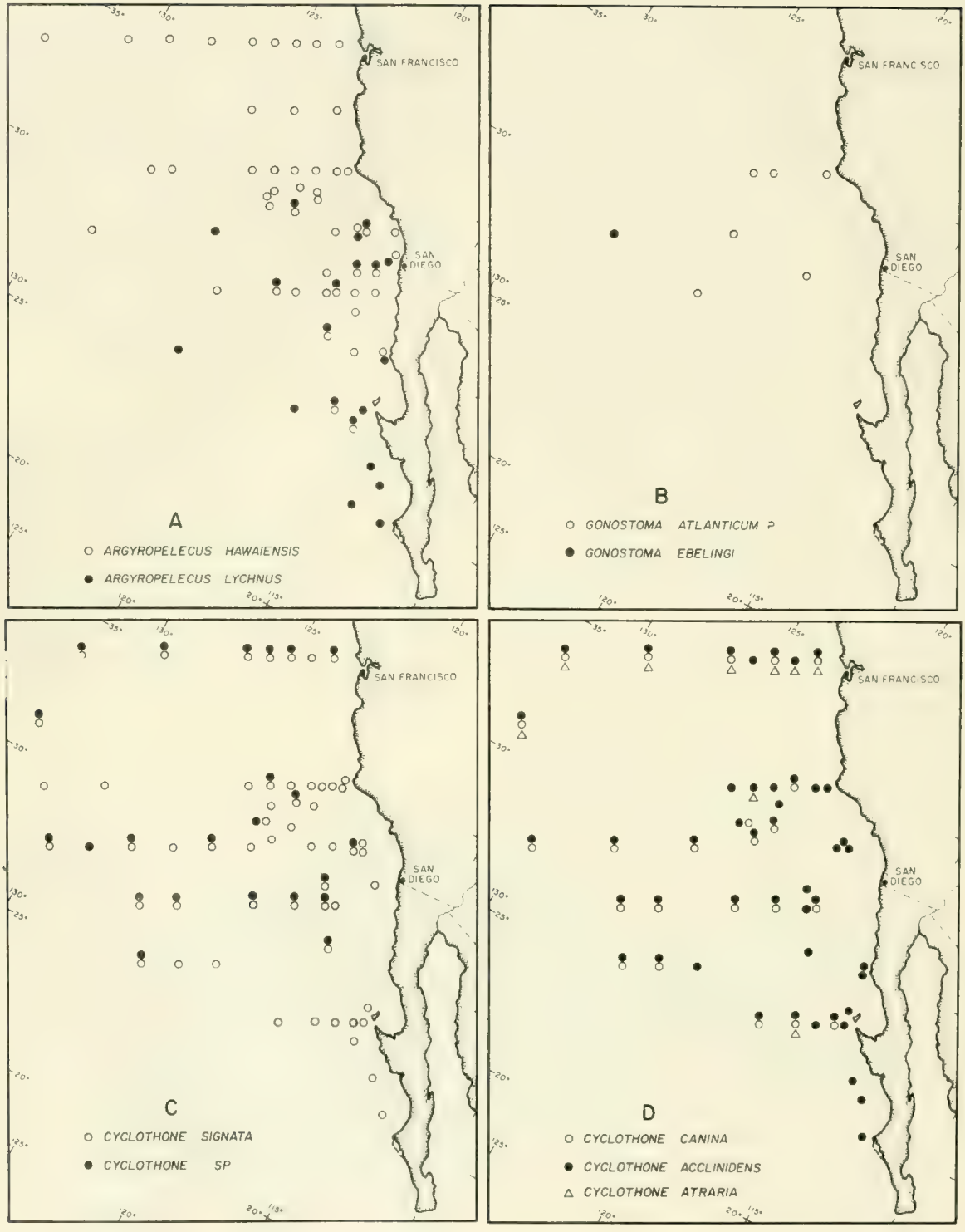

FIGURE 13.—Locations of capture of: A, *Argyropelecus hawaiensis*, *Argyropelecus lychnus*. B, *Gonostoma atlanticum?*, *Gonostoma ebelingi*. C, *Cyclothone signata*, *Cyclothone sp.* D, *Cyclothone canina*, *Cyclothone acclinidens*, *Cyclothone atraria*.

Our first attempts to identify the abundant specimens of *Cyclothone* in the survey collections by literature existing at that time were unsatisfactory. A detailed examination was made of this group, and the results and conclusions are summarized below. At least five species of *Cyclothone* are represented in our collections.

Some of the specimens of *C. signata* from the more offshore localities may represent the tersely described and inadequately known *C. alba* Brauer (B. N. Kobayashi, personal communication).

The form we designate as *Cyclothone* sp. (number 33) may be an undescribed species. There is a possibility that it represents *C. pseudopallida*, recently described by Mukhacheva (1964) (B. N. Kobayashi, personal communication).

Although *Cyclothone microdon* (Günther) has been reported from California waters, none of the specimens taken in the survey can be definitely attributed to this species. *C. pallida* Brauer has also been reported off California, but we find that the form here closely resembles Gilbert's description of *C. canina* (1905:604); especially significant is Gilbert's description of the palatine and pterygoid teeth of *C. canina*—"palatine teeth confined to the anterior end, in two small detached groups—pterygoid teeth all small, forming a single, somewhat irregular series." Actually his two small detached groups of palatines were one group (anterior) of palatines and one group (posterior) of pterygoids, as is typical of the genus. The irregular series of pterygoid teeth is thus far unique in this genus. They lie along the upper edge of the bone for nearly its entire length (fig. 14 C); however, the size and number of these teeth may be intraspecifically variable. As mentioned, this fact alone separates *C. canina* from other California species, and, unless the type specimens of *C. pallida* are found to contain such an arrangement of teeth (all other characters being equal), the two forms must certainly stand as distinct.

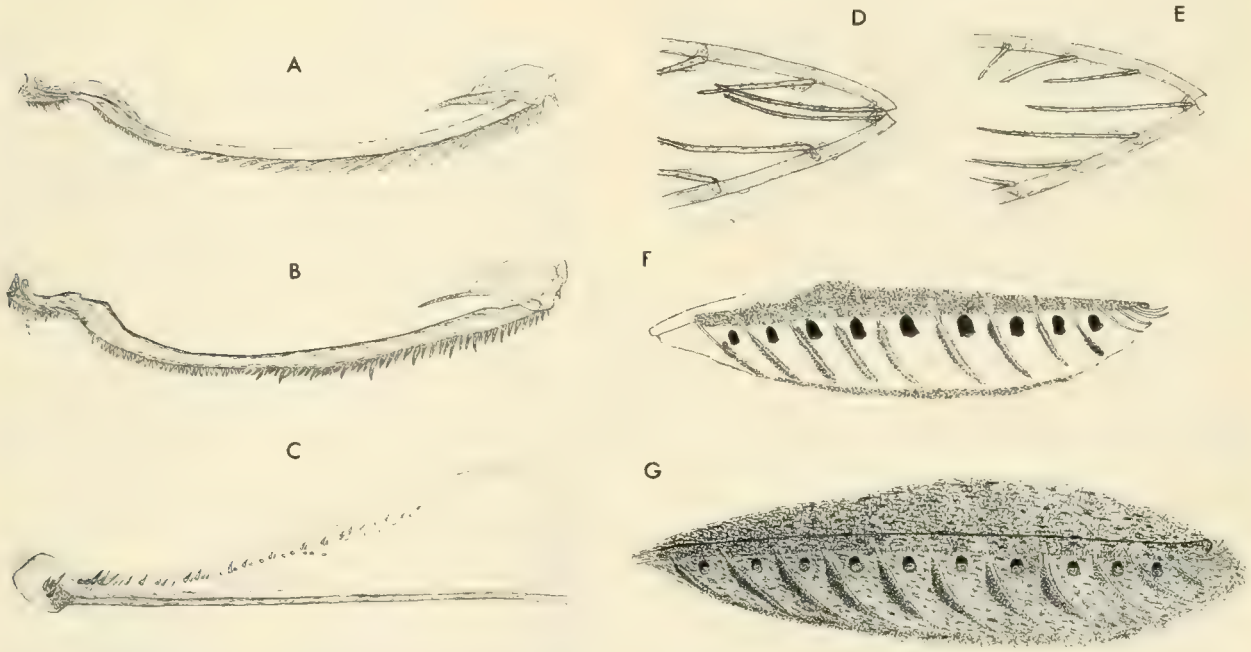

FIGURE 14.—*Cyclothone*. A, upper jaw of *C. acclinidens* showing the arrangement of teeth along the maxillary and premaxillary; the premaxillary is at the extreme left; the long slender bone possessing most of the teeth is the maxillary; and the small bone at upper right is the supramaxillary. B, upper jaw of *C. canina*. C, palatine and pterygoid bones of *C. canina* showing the unique row of teeth on the entopterygoid; the anterior end is at the left. D, posterior part of the first gill arch of *Cyclothone* sp. showing the typical arrangement of two gillrakers at the angle. E, posterior part of the first gill arch of *C. signata* showing the unique arrangement of only one gillraker at the angle of the epibranchial and ceratobranchial bones. F, branchiostegal membrane and rays of *C. signata* showing photophore and pigment arrangement. G, branchiostegal membrane and rays of *C. acclinidens* showing photophore and pigment arrangement.

All California species posses a photophore immediately below the eye and slightly forward of the eye's midline, a photophore above the posterior extremity of the maxillary on a level with the eye, and a photophore immediately behind the angle of the preopercle. Other photophores are mentioned in table 2. The photophores between the bases of the pelvic and anal fins have not been dealt with as a separate unit because an exact dividing line between these and the anal-to-caudal group is difficult to determine in many fish. Generally, *C. signata* has four photophores between the pelvics and anal and the other species have five. The first two pairs in this group are markedly close-set in *Cyclothone* sp., while the interspaces are equal or slightly greater posteriorly in the other species.

KEY TO ADULTS OF THE CALIFORNIA AND BAJA CALIFORNIA SPECIES OF THE GENUS *CYCLOTHONE*

I. Branchiostegal membranes without pigment except for a thin line over all but a few of the most posterior rays and along the upper and lower margins (fig. 14F). Roof of mouth pigmented mainly along its midline. Gill cavities nearly colorless. Gillrakers totaling less than 20 on the lateral side of the first gill arch. One or two gillrakers at angle of first gill arch.

A. Total gillrakers on lateral side of first gill arch not more than 15 (usually 4+10). Only one gillraker at angle of first gill arch (fig. 14E). ---------- ----------*C. signata* Garman.

B. Total gillrakers on lateral side of first arch 17–19 (the position of the medial rakers on the arch accentuated by a thin pigment line). Two gillrakers at angle of first gill arch (fig. 14D).---*Cyclothone* sp.

II. Entire branchiostegal membranes and most of the oral and gill cavities darkly pigmented (fig. 14G). Gillrakers more than 20 on the lateral side of the first gill arch. Two gillrakers at angle of first gill arch.

A. None of the teeth on the premaxillary directed strongly anterioventrad; generally, every third or fourth of the oblique teeth enlarged; canines conspicuous on premaxillary (fig. 14B). Entopterygoid teeth not confined to an anterior cluster (fig. 14C. ----------*C. canina Gilbert.*

B. Teeth along posterior three quarters of maxillary directed strongly anterioventrad, generally increasing in obliqueness and decreasing in size anteriorly; no conspicuous canines on the premaxillary (fig. 14A). Entopterygoid teeth confined to an anterior cluster.

1. Branchiostegal photophores 8 or 9. Branchiostegal rays 12. Pigmentation dark brown and usually persistent; photophores relatively small; scale pockets conspicuous. ----*C. atraria* Gilbert.

2. Branchiostegal photophores 10 or 11. Branchiostegal rays 14. Pigmentation light brown or greyish; photophores of relatively moderate size; scale pockets not conspicuous. ---------- ----------*C. acclinidens* Garman.

32. *Cyclothone canina* Gilbert.

Figures 13D, 14B, and 14C.

60.60, H6204, (3) 24–61 mm.; 60.80, H6204, (1) 62 mm.; 60.100, H6204, (4) 24–48.5 mm.; 60.140, H6204, (3) 24–49 mm.; 60.180, H6204, (6) 22–70 mm.; 70.200, H6204, (2) 24.5–63.5 mm.; 80.70, H6204, (1) 56 mm.; 86.92, C6303,

TABLE 2.—*Comparative morphological data for the five species of* Cyclothone *occurring off the coasts of California and Baja California*

Morphological character	Species				
	signata	Sp. No. 33	*canina*	*acclinidens*	*atraria*
Dorsal rays	13–14	13–15	14–15	13–15	13–14.
Anal rays	19–20	19–21	18–19	18–20	18–19.
Pectoral rays	8–10	9	11	9–10	9–10.
Pelvic rays	6	6	6	6	6.
Branchiostegal rays	13	14	14	14	12.
Gillrakers	3–4 +9–10	6–7+11–12	9–10+14–16	7–8+14–15	8–9+14.
Vertebrae	13+18–19	12–13+19–20	13+18–19	13+18	13+19.
Photophores:					
Branchiostegal	8–9	9–11	9–10	10–11	8–9.
Lateral	7	7+1 or 7+2	7+1 or 7+2	7+2	7+2.
Isthmus to pelvic	13	13	13	13	13.
Pelvic to caudal	18	20–21	20–21	18–19	19–21.
Relative size	Small	Moderate	Large	Large	Moderately large.
Body shape	Moderately slender	Very slender	Slender	Moderately slender	More robust than others.
General body color	Pale—rarely pigment flecks on flanks.	Pale or flanks brown	Flanks brown	Brown flanks or grey cast.	Dark brown.
Pigment visible between interneurals and interhaemals.	Yes	Yes	Yes	Yes	No.
Premaxillary teeth	Slight irregular	Irregular	2–4 distinct canines	Irregular, nearly forming canines.	Irregular, nearly forming canines.
Slope of maxillary teeth	Moderate	Moderate	Moderate	Very strong	Strong.
Vomerine teeth	Usually absent, minute if present.	Present	Present	Present	Present.
Position of anus between pelvics and anal	Immediately behind pelvic base	Much nearer pelvics than anal	Midway	Midway or less	Midway.
Scale pockets conspicuous	No	No	No	No	Yes.
Number of rakers at angle of first gill arch	1	2	2	2	2.

(4) 31.5–57 mm.; 87.80, C6303, (1) 58.5 mm.; 87.90, C6303, (1) 43.5 mm.; 90.120, H6204, (3) 43–58 mm.; 90.160, H6204, (4) 31–59 mm.; 90.200, H6204, (9) 30.5–58.5 mm.; 100.60, H6204, (6) 52–62 mm.; 100.80, H6204, (2) 41–51.5 mm.; 100.100, H6204, (5) 40–62 mm.; 100.140, H6204, (4) 31–59 mm.; 100.160, H6204, (6) 47–60 mm.; 110.140, H6204, (2) 25–33 mm.; 110.160, H6204, (8) 28–60 mm.; 120.50, H6204, (2) 56–58 mm.; 120.70, H6204, (1) 44 mm.; 120.90, H6204, (4) 42–62 mm.

33. *Cyclothone* sp.

Figures 13C and 14D.

60.60, H6204, (8) 27–42.5 mm.; 60.80, H6204, (16) 18–47 mm.; 60.90, H6204, (6) 19–31.5 mm.; 60.100, H6204, (34) 24–47 mm.; 60.140, H6204, (11) 26–47.5 mm.; 60.180, H6204, (27) 15–46 mm.; 70.200, H6204, (20) 21.5–42 mm.; 80.90, H6204, (2) 35–37.5 mm.; 83.77, C6303, (6) 32–45 mm.; 86.92, C6303, (7) 27–37.5 mm.; 90.48a, H6105, (3) 36.5–41 mm.; 90.120, H6204, (7) 30.5–36 mm.; 90.160, H6204, (4) 12–36 mm.; 90.180, H6204, (1) 28.5 mm.; 90.200, H6204, (11) 20–38 mm.; 97.65, C6303, (2) 27 mm.; 100.65, C6303, (1) 26.5 mm.; 100.80, H6204, (6) 35.5–41.5 mm.; 100.100, H6204, (4) 36–38.5 mm.; 100.140, H6204, (9) 18–40 mm.; 100.160, H6204, (9) 29–38.5 mm.; 108.63, C6303, (1) 27 mm.; 110.160, H6204, (2) 35–40 mm.

34. *Cyclothone signata* Garman.

Figures 13C, 14E, and 14F.

60.60, H6204, (95) 19–36 mm.; 60.60, C6208, (1) 26 mm.; 60.70, H6204, (7) 19–30 mm.; 60.80, H6204, (108) 15–36 mm.; 60.90, H6204, (9) 24–29 mm.; 60.100, H6204, (99) 14–38.5 mm.; 60.140, H6204, (128) 13.5–36 mm.; 60.180, H6204, (97) 16–34 mm.; 70.200, H6204, (83) 18.5–34.5 mm.; 79.54, B6303, (9) 16.5–29.5 mm.; 80.55, H6204, (23) 19–29 mm.; 80.60, H6204, (49) 16–31 mm.; 80.70, H6204, (98) 12.5–34.5 mm.; 80.70, C6208, (1) 22.5 mm.; 80.75, B6303, (1) 20 mm.; 80.80, H6204, (37) 14–32 mm.; 80.90, H6204, (152) 17–34 mm.; 80.100, H6204, (93) 20–30 mm.; 80.170, C6208, (1) 24 mm.; 80.200, H6204, (1) 28.5 mm.; 83.77, C6303, (114) 21.5–33 mm.; 83.90, C6303, (67) 17.5–30 mm.; 84.70, C6303, (1) 28 mm.; 86.92, C6303, (73) 21–34 mm.; 87.80, C6303, (3) 24.5–33.5 mm.; 87.90, C6303, (2) 28–38 mm.; 90.45a, H6105, (16) 23.5–33.5 mm.; 90.48a, H6105, (132) 16–33 mm.; 90.48b, H6105, (9) 20–30 mm.; 90.60, H6204, (2) 24–38 mm.; 90.60, C6208, (21) 16–26 mm.; 90.70, H6204, (1) 21 mm.; 90.70, C6208, (15) 21.5–32.5 mm.; 90.100, C6208, (17) 17–26 mm.; 90.120, H6204, (92) 12.5–36 mm.; 90.140, H6204, (1) 19.5 mm.; 90.140, C6208, (1) 25 mm.; 90.160, H6204, (51) 16–32.5 mm.; 90.160, C6208, (1) 30 mm.; 90.200, H6204, (41) 15–33 mm.; 97.40, C6303, (21) 22–30 mm.; 97.65, C6303, (94) 17.5–38 mm.; 100.60, H6204, (6) 25–33 mm.; 100.65, C6303, (409) 17–35 mm.; 100.80, H6204, (91) 17–36 mm.; 100.100, H6204, (29) 10–34.5 mm.; 100.140, H6204, (22) 18.5–35 mm.; 100.160, H6204, (31) 17.5–35.5 mm.; 108.63, C6303, (149) 19.5–36 mm.; 110.35, C6303, (3) 26–30 mm.; 110.46, C6303, (29) 23–33 mm.; 110.120, H6204, (25) 22–35 mm.; 110.140, H6204, (13) 18–28.5 mm.; 110.160, H6204, (33) 16–32 mm.; 111.37b, C6303, (9) 25–30 mm.; 118.43, B6212, (24) 21.5–33.5 mm.; 120.45, H6204, (12) 20–29 mm.; 120.50, H6204, (2) 27–32 mm.; 120.60, H6204, (4) 25–30 mm.; 120.70, H6204, (8) 22.5–33 mm.; 120.90, H6204, (16) 22.5–32 mm.; 123.50, B6203, (1) 22 mm.; 130.40, B6212, (5) 22.5–26.5 mm.; 140.35, B6212, (14) 23.5–32 mm.

35. *Cyclothone acclinidens* Garman.

Figures 13D, 14A, and 14G.

60.60, H6204, (33) 15–54.5 mm.; 60.70, H6204, (3) 27–42.5 mm.; 60.80, H6204, (13) 26–55.5 mm.; 60.90, H6204, (1) 34 mm.; 60.100, H6204, (10) 28–55 mm.; 60.140, H6204, (37) 27–56.5 mm.; 60.180, H6204, (7) 31.5–58 mm.; 70.200, H6204, (5) 30.5–40 mm.; 80.55, H6204, (41) 20–40 mm.; 80.60, H6204, (4) 21–46 mm.; 80.70, H6204, (23) 22.5–58 mm.; 80.80, H6204, (1) 31 mm.; 80.90, H6204, (66) 20.5–57 mm.; 80.100, H6204, (32) 21–45.5 mm.; 83.77, C6303, (86) 21–37 mm.; 84.70, C6303, (4) 35–53 mm.; 86.92, C6303, (141) 26.5–56 mm.; 87.80, C6303, (57) 30–55 mm.; 87.90, C6303, (6) 32.5–50 mm.; 90.45a, H6105, (71) 23.5–43.5 mm.; 90.48a, H6105, (207) 15.5–43.5 mm.; 90.48b, H6105, (10) 16.5–24.5 mm.; 90.120, H6204 (29) 19–56 mm.; 90.160, H6204, (6) 32.5–50.5 mm.; 90.200, H6204, (16) 23–58 mm.; 95.31a, B6204, (2) 26–31 mm.; 97.65, C6303, (7) 17.5–32 mm.; 100.60, H6204, (98) 20.5–53 mm.; 100.65, C6303, (12) 25–45.5 mm.; 100.80, H6204, (62) 23–58 mm.; 100.100, H6204, (65) 14–56 mm.; 100.140, H6204, (18) 25.5–54 mm.; 100.160, H6204, (16) 24–57 mm.; 108.63, C6303, (12) 18–34 mm.; 110.35, C6303, (1) 26 mm.; 110.46, C6303, (3) 22–27 mm.; 110.120, H6204, (88) 19–56 mm.; 110.140, H6204, (11) 19–35 mm.; 110.160, H6204, (35) 16–56 mm.; 111.37b, C6303, (5) 17–30 mm.; 118.43, B6212, (16) 17.5–31 mm.; 120.45, H6204, (4) 21.5–25.5 mm.; 120.50, H6204, (174) 17–51 mm.; 120.60, H6204, (1) 25 mm.; 120.70, H6204 (152) 14.5–55 mm.; 120.90, H6204, (276) 19.5–63 mm.; 130.40, B6212, (81) 13.5–38.5 mm.; 133.35, B6212, (3) 17–22 mm.; 140.35, B6212, (77) 14–40 mm.

36. *Cyclothone atraria* Gilbert.

Figure 13D.

60.60, H6204, (4) 36.5–50 mm.; 60.70, H6204, (1) 51 mm.; 60.80, H6204, (5) 21–49.5 mm.; 60.100, H6204, (6) 31–56 mm.; 60.140, H6204, (6) 37.5–51.5 mm.; 60.180, H6204, (11) 28–51 mm.; 70.200, H6204, (9) 28–54.5 mm.; 80.90, H6204, (1) 55 mm.; 120.70, H6204, (1) 53.5 mm.

37. *Diplophos* sp.

133.35, B6212, (1) 50 mm.

It is not possible to identify this slightly damaged specimen specifically from the revision by Grey (1960:57–125).

38. *Valenciennellus tripunctulatus* (Esmark)?

Figure 15A.

70.200, H6204, (1) 28 mm.; 73.200, B6203, (2) 25 mm.; 90.120, H6204, (1) dis. adult; 90.160, H6204, (1) ca. 10 mm.; 90.180, H6204, (1) 25 mm.; 90.200, H6204, (1) 25.5 mm.

This specific identification is questioned because most of these specimens have four groups of anal

to caudal (AC) photophores rather than the five groups reportedly characteristic for *V. tripunctulatus;* this difference may indicate that these specimens are actually *V. stellatus* Garman. This problem was discussed by Grey (1960: 68).

39. *Danaphos oculatus* (Garman).

Figure 15A.

60.60, H6204, (1) 19.5 mm.; 60.70, H6204, (7) 20–25 mm.; 60.80, H6204, (4) 22–38 mm.; 60.90, H6204, (7) 20.5–31 mm.; 60.90, C6208, (2) 32 mm.; 60.100, H6204, (2) 22.5–23.5 mm.; 60.120, H6204, (21) 29–40 mm.; 60.160, B6203, (3) 34.5–36 mm.; 60.160, H6204, (1) 31 mm.; 60.180, H6204, (1) 40 mm.; 70.60, C6208, (1) 23 mm.; 70.200, H6204, (1) 44 mm.; 80.55, H6204, (3) 30–30.5 mm.; 80.60, H6204, (1) 27 mm.; 80.70, H6204, (3) 26.5–38.5 mm.; 80.75, B6303, (1) 22.5 mm.; 80.80, H6204, (14) 26–39 mm.; 80.90, H6204, (7) 24–38 mm.; 80.100, H6204, (3) 30–32 mm.; 80.140, C6208, (1) 30 mm.; 83.77, C6303, (44) 27–40 mm.; 83.90, C6303, (61) 23–40.5 mm.; 84.67, C6303, (3) 29–30 mm.; 86.92, C6303, (4) 28–30 mm.; 87.80, C6303, (4) 34.5–40 mm.; 90.32, B6203, (2) 33 mm.; 90.45a, H6105, (1) 32.5 mm.; 90.60, H6204, (1) adult, damaged; 90.70, H6204, (4) 31–37 mm.; 90.110, B6203, (1) 36 mm.; 90.120, H6204, (1) 31 mm.; 90.140, C6208, (2) 24–30.5 mm.; 90.160, H6204, (1) 37.5 mm.; 97.65, C6303, (3) 20.5–39 mm.; 100.60, H6204, (1) 34 mm.; 100.65, C6303, (18) 25.5–39 mm.; 100.80, H6204, (9) 31–35 mm.; 100.90, H6204, (1) 34 mm.; 100.160, H6204, (1) 32.5 mm.; 108.63, C6303, (5) 29–38 mm.; 110.120, H6204, (2) 25–35 mm.; 110.140, H6204, (1) 29 mm.; 110.160, H6204, (2) 32.5–35 mm.; 120.45, H6204, (1) 29 mm.; 120.60, H6204, (1) 32 mm.; 120.70, H6204, (1) 34 mm.; 140.35, B6212, (1) 34 mm.

40. *Vinciguerria nimbaria* (Jordan and Williams).

Figure 15B.

60.200a, B6203, (2) 24.5–38 mm.; 73.200, B6203, (1) 39 mm.; 80.140, C6208, (1) 23.5 mm.; 80.170, C6208, (2) 16–22 mm.; 90.110, C6303, (4) 20–43 mm.; 90.150, C6208, (10) all ca. 26 mm.; 90.160, H6204, (2) 18–19.5 mm.; 90.180, H6204, (1) 39.5 mm.; 93.100, C6303, (1) 21.5 mm.; 100.140, H6204, (1) 20 mm.; 100.160, H6204, (1) 26 mm.

41. *Vinciguerria lucetia* (Garman).

Figure 15B.

83.77, C6303, (1) 34 mm.; 83.90, C6303, (1) 35.5 mm.; 87.80, C6303, (1) 42 mm.; 90.48b, H6105, (1) ca. 10 mm.; 90.120, C6208, (5) 16.5–28 mm.; 90.140, H6204, (1) 49.5 mm.; 90.150, C6208, (7) 17–19 mm.; 100.100, H6204, (3) 32.5–42 mm.; 100.160, H6204, (1) 24 mm.; 110.100, H6204, (1) 24 mm.; 110.120, H6204, (3) 28–44 mm.; 110.140, H6204, (1) 19 mm.; 120.45, B6212, (24) 17–22.5 mm.; 120.60, H6204, (4) 34–36 mm.; 120.70, H6204, (4) 28–41 mm.; 120.80, H6204, (10) 31.5–47 mm.; 120.90, H6204, (19) 27.5–49 mm.; 123.45, B6212, (158) 18–44.5 mm.; 123.50, B6203, (3) 22–27 mm.; 127.45, B6212, (7) 21–32.5 mm.; 130.40, B6212, (142) 15–56.5 mm.; 133.35, B6212, (87) 15.5–53.5 mm.; 137.35, B6212, (536) 12.5–48.5 mm.; 137.50, B6203, (7) 28.5–52 mm.; 140.35, B6212, (388) 14.5–50 mm.

42. *Vinciguerria poweriae* (Cocco).

Figure 15B.

60.120, B6203, (2) 24–28 mm.; 60.160, B6203, (1) 26 mm.; 60.180, B6203, (1) 24.5 mm.; 60.200, H6204, (1) 31 mm.; 70.200, H6204, (1) 18 mm.; 73.200, B6203, (2) 27–30 mm.; 80.140, C6208, (2) 23–23.5 mm.; 80.200, C6208, (1) 34 mm.; 83.77, C6303, (2) 23–28 mm.; 90.110, C6303, (8) 26–33.5 mm.; 90.120, C6208, (2) 17.5 mm.; 90.124, C6208, (2) 16 mm.; 90.160, H6204, (2) 17.5–18 mm.; 90.160, C6208, (1) 27.5 mm.; 90.200, H6204, (1) 17.5 mm.; 92.115, B6303, (1) 18.5 mm.

The specimens from station 83.77 are closer to the continent (about 195 km. (120 miles) offshore) than is usual for this species (see Ahlstrom and Counts 1958, fig. 25).

43. *Vinciguerria* sp.

90.140, C6208, (3) 18–20 mm.

These damaged specimens are unidentifiable to species.

44. *Ichthyococcus elongatus* Imai.

Figure 15C.

80.70, H6204, (1) 65 mm.

This record extends the known range of the species from Japan and lat. 41°42′ N., long. 150° 00′ W. to near the coast of California and also extends its geographical range into that of *I. irregularis* as described by Rechnitzer and Böhlke (1958).

45. *Ichthyococcus irregularis* Rechnitzer and Böhlke.

Figure 15C.

90.47, C6208, (1) 37 mm.; 100.60, H6204, (1) 61.5 mm.; 108.63, C6303, (1) 51 mm.; 120.90, H6204, (1) 41 mm.

STOMIATIDAE

46. *Stomias atriventer* Garman.

Figure 15D.

82.69, C6303, (1) 59 mm.; 84.70, C6303, (1) 209 mm.; 86.92, C6303, (5) 52.5–227 mm.; 87.80, C6303, (2) 195–218 mm.; 87.90, C6303, (1) 74 mm.; 90.45a, H6105, (1) 202 mm.; 90.48a, H6105, (1) 116 mm.; 90.110, C6303, (1) 228 mm.; 95.31a, B6204, (1) 158 mm.; 97.40, C6303, (1) 232 mm.; 97.65, C6303, (1) 45 mm.; 100.40, H6204, (3) 122–204 mm.; 100.40, C6303, (1) 161 mm.; 100.100, H6204, (1) 29 mm.; 108.63, C6303, (24) 128–235 mm.; 110.35, C6303, (3) 123–205 mm.; 110.40, H6204, (1) 142 mm.; 110.46, C6303, (7) 180–226 mm.; 120.45, H6204, (8) 138–214 mm.; 120.45, B6212, (1) 48 mm.; 120.50, H6204, (1) 212 mm.; 120.60, H6204, (1) 131 mm.; 120.80, H6204, (1) 186 mm.;

FIGURE 15.—Locations of capture of: A, *Valenciennellus tripunctulatus?*, *Danaphos oculatus*. B, *Vinciguerria nimbaria*, *Vinciguerria lucetia*, *Vinciguerria poweriae*. C, *Ichthyococcus elongatus*, *Ichthyococcus irregularis*. D, *Stomias atriventer*, *Stomias* sp., *Chauliodus macouni*.

123.50, B6203, (7) 83.5–214 mm.; 137.35, B6212, (1) 49 mm.; 137.50, B6203, (2) 127–178 mm.

This species was listed as a subspecies of *Stomias boa* (Risso) by Ege (1934:23) but is now generally regarded as a distinct species. In a few of the 78 specimens collected during the survey, the barbel was broken off, but the normal three equal-sized filaments at the end of the barbel were present in the others, except one. On the exceptional specimen, one of the three filaments was branched to near its base, giving the superficial appearance of four filaments at the end of the barbel.

47. *Stomias* sp.

Figure 15D.

110.35, H6204, (1) 189 mm.

This specimen, occurring within the range of *S. atriventer*, represents either a morphological variant or an undescribed species. It differs in a number of characters from *S. atriventer* and from all known species of *Stomias* in having six equal-sized filaments, each with a separate base, at the end of the barbel.

MELANOSTOMIATIDAE

48. *Leptostomias* sp.

90.200, C6208, (1) 186 mm.

This specimen was taken about 1,000 km. (620 miles) WSW. of Point Conception, Calif. The number and taxonomic limits of the species of this genus are uncertain, and this specimen is not specifically identified, pending needed study of the genus.

49. *Opostomias mitsuii* Imai.

60.80, C6208, (1) 164 mm.; 83.77, C6303, (1) 77 mm.

These specimens, taken about 185 km. (115 miles) west of San Francisco and about 195 km. (120 miles) SE. of Point Conception, Calif., are the first of this species to be reported from waters off California. The three known species of this genus, including *O. micripnus* (Günther) and *O. gibsonpacei* Barnard, appear to be valid, but further comparison is necessary (R. H. Gibbs, personal communication).

50. *Flagellostomias boureei* Zugmayer.

80.80, H6204, (1) 134 mm.; 87.80, C6303, (1) 186 mm.

These specimens, taken about 200 and 210 km. (125 and 150 miles) off Point Conception, Calif., differ only slightly from the detailed description of *F. boureei* from the western Atlantic by Beebe and Crane (1939:179–185). Comparison of other Atlantic and Pacific specimens indicates that they are the same species (R. H. Gibbs, personal communication).

51. *Melanostomias valdiviae* Brauer.

86.92, C6303, (2) 163–175 mm.

These two specimens taken about 305 km. (190 miles) SSW. of Point Conception, and one specimen in the collections of Scripps Institution of Oceanography collected off San Juan Seamount, constitute the first records of this species in this area.

52. *Photonectes margarita* (Goode and Bean).

Figure 16A.

60.120, B6203, (1) 138 mm.; 60.160, H6204, (1) 171 mm.; 60.200, H6204, (2) 118–193 mm.; 80.90, H6204, (1) 135 mm.; 90.160, C6208, (1) 45 mm.; 93.100, C6303, (1) 138 mm.; 100.80, H6204, (1) 50.5 mm.; 100.120, H6204, (1) 91 mm.; 100.140, H6204, (1) 68 mm.

These specimens appear to be this species, redescribed from material from the North Atlantic by Beebe and Crane (1939:175–179). The above listed specimens vary considerably in several characters, especially barbel structure (at least some of this variation is ontogenetic). Although more than one species may be represented, the variation in barbel structure is thought to be intraspecific.

53. *Tactostoma macropus* Bolin.

Figure 16A.

60.60, H6204, (1) 175 mm.; 60.80, H6204, (1) 85 mm.; 60.80, C6208, (13) 54.5–325 mm.; 60.90, H6204, (3) 143–234 mm.; 60.90, C6208, (9) 135–247 mm.; 60.100, C6208, (1) 231 mm.; 60.120, B6203, (1) 232 mm.; 60.120, H6204, (1) 228 mm.; 66.100, C6208, (1) 200 mm.; 80.55, H6204, (2) 85.5–233 mm.; 80.60, H6204, (2) 91–231 mm.; 80.60, C6208, (2) 156–204 mm.; 80.90–5N, B6203, (2) 91–91.5 mm.; 80.130, C6208, (1) 44 mm.; 82.69, C6303, (1) 81 mm.; 83.77, C6303, (4) 63–163 mm.; 84.92, B6303, (2) 56–66 mm.; 86.92, C6303, (3) 210–293 mm.; 87.80, C6303, (1) 320 mm.; 88.105a, B6303, (1) 76 mm.; 90.60, C6208, (1) 101 mm.

54. *Bathophilus flemingi* Aron and McCrery.

Figure 16A.

60.80, C6208, (1) 64 mm.; 60.120, B6203, (1) 65 mm.; 66.100, C6208, (1) 41.5 mm.; 80.60, C6303, (3) 76–85 mm.; 80.90, H6204, (1) 72.5 mm.; 82.69, C6303, (1) 65 mm.; 84.67, C6303, (1) 84 mm.; 86.92, C6303, (1) 131 mm.; 87.200, B6203, (1) 36 mm.; 88.105b, B6303, (2) 68–82 mm.;

FIGURE 16.—Locations of capture of: A, *Photonectes margarita*, *Tactostoma macropus*, *Bathophilus flemingi*. B, *Idiacanthus antrostomus*, *Borostomias panamensis*, *Aristostomias scintillans*. C, *Hierops crockeri*, *Electrona rissoi*. D, *Hygophum* sp., *Tarletonbeania crenularis*.

90.140, H6204, (1) 56.5 mm.; 90.160, H6204, (1) 33 mm.; 97.40, C6303, (1) 97 mm.; 97.65, C6303, (4) 75–120 mm.; 100.65, C6303, (1) 70 mm.; 100.120, H6204, (1) 62 mm.; 100.140, H6204, (1) 67 mm.

B. flemingi was described as a new species from the Eastern North Pacific (Aron and McCrery, 1958:181), although it differed only slightly from the inadequately described *B. indicas* Brauer from the Indian Ocean. Recent evidence indicates that the two species may be synonymous (R. H. Gibbs, personal communication). We found a range in pelvic fin rays of 2 + 2 to 2 + 5 in several specimens counted.

55. Melanostomiatidae, unidentified.

60.180, H6204, (4) 18–30 mm.

These larval specimens have not been identified.

IDIACANTHIDAE

56. *Idiacanthus antrostomus* Gilbert.

Figure 16B.

60.80, H6204, (5) 53–118 mm.; 60.80, C6208, (1) 216 mm.; 60.90, H6204, (1) 207 mm.; 60.90, C6208, (1) 154 mm.; 60.100, H6204, (4) 65–79 mm.; 60.100, C6208, (1) 149 mm.; 60.120, B6203, (3) 168–269 mm.; 60.160, B6203, (1) 160 mm.; 60.180, H6204, (3) 62–124 mm.; 70.80b, B6203, (2) 100–137 mm.; 70.80–5N, B6203, (1) 121 mm.; 73.200, B6203, (1) dis.; 80.55, H6204, (1) 135 mm.; 80.70, H6204, (1) 67 mm. (larva); 80.100, B6203, (1) 241 mm.; 82.69, C6303, (2) 99–252 mm.; 83.77, C6303, (16) 64–348 mm.; 84.70, C6303, (1) 150 mm.; 84.92, B6303, (1) 115 mm.; 86.92, C6303, (17) 61–371 mm.; 87.80, C6303, (4) 66–266 mm.; 87.90, C6303, (4) 123–260 mm.; 88.105a, B6303, (1) 344 mm.; 90.48a, H6105, (2) 69–333 mm.; 90.60, H6204, (1) 73 mm.; 90.110, C6303, (4) 236–300 mm.; 90.120, H6204, (2) dis., 70 mm.; 90.140, H6204, (1) 95 mm.; 90.140, C6208, (2) 58–84 mm.; 90.150, C6208, (1) 125 mm.; 90.160, H6204, (1) 65 mm.; 90.160, C6208, (1) 73 mm.; 90.180, H6204, (1) 104 mm.; 90.200, H6204, (1) 42 mm.; 93.100, C6303, (4) 60–342 mm.; 97.40, C6303, (10) 66–320 mm.; 97.65, C6303, (1) 210 mm.; 100.60, H6204, (1) 249 mm.; 100.65, C6303, (8) 60.5–274 mm.; 100.80, H6204, (2) dis., 59 mm.; 100.90, H6204, (1) 233 mm.; 103.50, C6303, (1) 259 mm.; 108.63, C6303, (9) 134–343 mm.; 110.46, C6303, (3) 209–348 mm.; 110.35, C6303, (8) 156–212 mm.; 110.120, H6204, (1) 98 mm.; 110.160, H6204, (2) 77–115 mm.; 120.80, H6204, (1) 292 mm.; 123.45, B6212, (1) 144 mm.; 123.50, B6203, (7) 178–292 mm.

This is probably the only species of this genus that occurs in the eastern Pacific; as *I. panamensis* Regan and Trewavas, described from the Gulf of Panama, may be a junior synonym of *I. antrostomus* (R. H. Gibbs, personal communication). An adult male of 70 mm. SL from station 60.80, H6204 is larger than maximum sizes of males reported as 44 mm. (adult) and 48 mm. (postlarva) by Beebe (1934:234–236). This was the most abundant and ubiquitous of the 12 species of the suborder Stomiatoidei taken on the survey.

ASTRONESTHIDAE

57. *Borostomias panamensis* Regan and Trewavas.

Figure 16B.

80.90, H6204, (1) 244 mm.; 84.70, C6303, (1) 195 mm.; 86.92, C6303, (4) 85–270 mm.; 90.45, H6105, (1) 218 mm.; 90.48a, H6105, (1) 111 mm.; 120.90, H6204, (1) 186 mm.

B. macristius and *B. panamensis*, both described as new species from the Gulf of Panama by Regan and Trewavas (1929: 26–27), are synonymous (R. H. Gibbs, personal communication). According to specimens taken by this survey and in the collections of Scripps Institution of Oceanography, *B. panamensis* ranges at least from the Gulf of Panama to SSE. of Point Conception, Calif.

CHAULIODONTIDAE

58. *Chauliodus macouni* Bean.

Figures 15D and 17.

60.60, H6204, (5) 27.5–184 mm.; 60.80, H6204, (1) 39 mm.; 60.80, C6208, (1) 120 mm.; 60.90, C6208, (1) 68 mm.; 60.100, H6204, (2) 36–53 mm.; 60.140, H6204, (1) 36 mm.; 80.55, H6204, (3) 32–127 mm.; 80.70, H6204, (1) 26 mm.; 80.70, C6208, (1) dis.; 80.90, H6204, (2) 35.5–36 mm.; 80.100, H6204, (1) 31 mm.; 83.77, C6303, (3) 32–36 mm.; 83.90, C6303, (4) 51–64 mm.; 84.67, C6303, (1) 32.5 mm.; 84.70, C6303, (3) 33–198 mm.; 86.92, C6303, (5) 162–213 mm.; 87.80, C6303, (7) 169–204 mm.; 87.90, C6303, (5) 184–207 mm.; 90.60, H6204, (1) 40 mm.; 90.110, C6303, (2) 162–171 mm.

The genus *Chauliodus* has been revised by Regan and Trewavas (1929), Ege (1948), and Morrow (1961). Only two species of *Chauliodus* are known in the eastern Pacific. *C. barbatus* Garman ranges from Peru (Morrow, 1961:270) northward to about 1,770 km. (1,100 miles) SE. of southern Baja California (lat. 13°01′ N., long 127°11′ W., SIO 60–215). *C. macouni* ranges from Japan, the southern part of the Bering Sea, and through the Gulf of Alaska (Morrow, 1961:275–276) southward to the offshore waters of northern Baja California (station 90.110, C6303). With one exception, all evidence points to a geographic separation of these two species, about 1,770 km. (1,100 miles) separating their known ranges.

The one exception is a single specimen recorded by Ege (1948:108) as *C. macouni* from lat. 0°18′

S., long. 99°07′ W., near the Galapagos Island. Ege also reported three specimens of *C. barbatus* from the same station (3558). Morrow (1961: 256), on the basis of a partial reexamination of the excepted specimen, stated that "the Dana specimen of *C. macouni* does not appear to have been mis-identified." Yet nowhere is this specimen so adequately described, or compared with specimens from the usual range of *C. macouni*, that it can confidently be considered to be *C. macouni*, in view of the known occurrence of all other specimens of *C. macouni*.

Regan and Trewavas (1929:32 and 34) stated that in *C. sloani* Bloch and Schneider and in *C. danae* Regan and Trewavas the proportion of the eye diameter into the length of the lower jaw is "larger in male than female." We have determined that external morphological sexual dimorphism exists in *C. macouni*. Of 20 of the larger specimens taken on cruise C6303 (stations 84.70, 86.92, 87.80, 89.90, and 90.110), 8 are females with large ovarian eggs, ranging from 183–207 mm. SL (mean size 197), and 12 are males, 162–202 mm. (mean 177). The males have larger eyes than the females (eye into head 3.3 to 3.8 in the males, 4.0 to 4.6 in the females). One of the most pronounced differences between the sexes is the relative size and shape of the postocular organ. Morrow (1961:273) found that in *C. macouni* the postocular organ was generally elongate and triangular; the exposed luminous portion was triangular or at least pointed behind, while in other species of *Chauliodus* the postocular photophore was round or nearly so. His characterization is descriptive of the postocular organ of male specimens of *C. macouni*, especially of the exposed luminous portion, but in the females the organ is different and more variable than in the males. The organ is always smaller in the adult females. In some females the exposed luminous portion is reduced to a small rounded area, less than one-quarter of the area of that in the adult males; in others it is elongated, probably owing to a differential contraction following preservation of the surrounding tissue (fig. 17).

MALACOSTEIDAE

59. *Aristostomias scintillans* Gilbert.

Figures 16B and 18.

60.60, H6204, (1) 56 mm.; 60.80, C6208, (8) 73–214 mm.; 60.90, C6208, (2) 62–168 mm.; 60.120, H6204, (1) 189 mm.; 60.180, H6204, (1) 55.5 mm.; 70.80b, B6203, (4) 52–64 mm.; 70.80–5N, B6203, (6) 55–70 mm.; 80.90, B6203, (1) 78.5 mm.; 80.90–5N, B6203, (2) 64–67 mm.; 83.77, C6303, (1) 92 mm.; 86.92, C6303, (1) 54 mm.; 88.105a, B6303, (1) 58 mm.; 90.70, C6208, (1) 148 mm.; 90.80, C6208, (1) 51.5 mm.; 97.40, C6303, (4) 44–140 mm.; 97.50, B6203, (2) 82–129 mm.; 100.40, H6204, (1) 114 mm.; 108.63, C6303, (2) 46–109 mm.; 110.40, H6204, (1) 123 mm.; 120.80, H6204, (1) 101 mm.

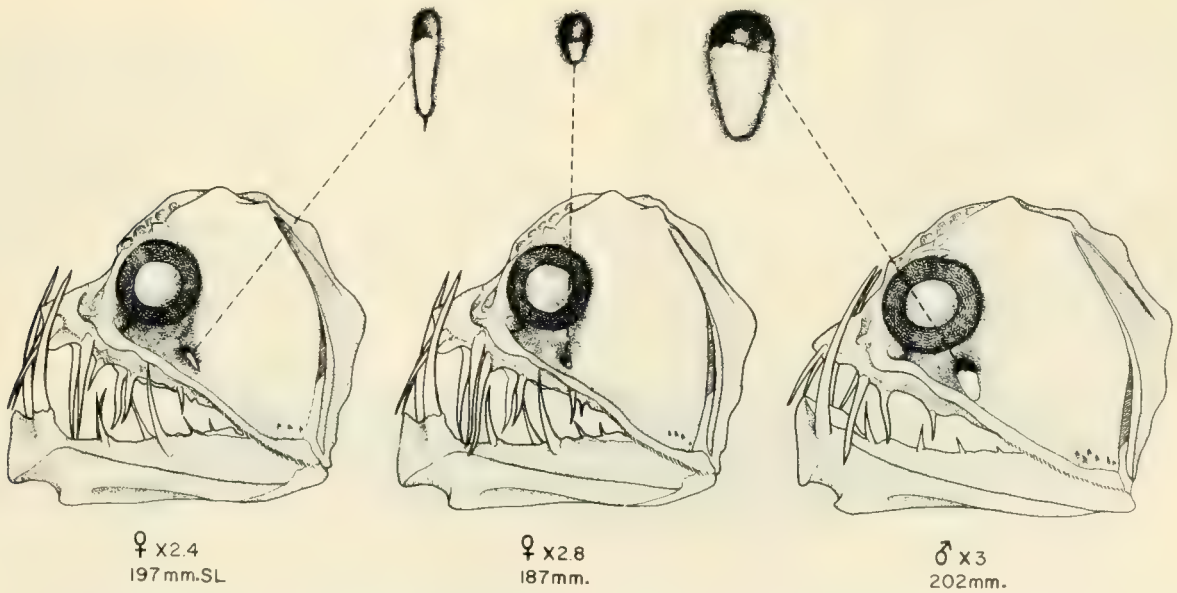

FIGURE 17.—*Chauliodus macouni*, postocular organs, showing the typical triangular shape in juveniles and adult males (right) and the variable and frequently elongated shape in adult females (left and middle).

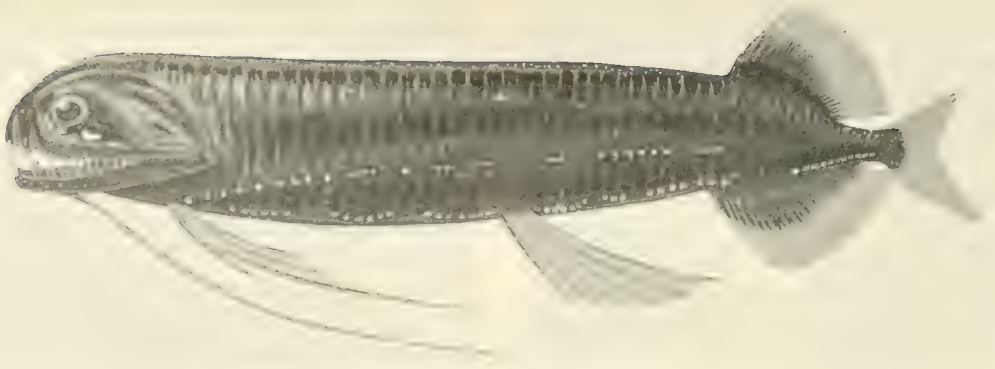

FIGURE 18.—*Aristostomias scintillans*, adult, ca. 280 mm. SL, station 20.40, B5003.

BATHYLACONIDAE

60. *Bathylaco nigricans* Goode and Bean.

Figure 19.

86.92, C6303, (1) 244 mm.

The four previously known specimens of this rare isospondylid (including *Macromastax gymnus* Beebe) were compared by Maul (1959:1–8). G. E. Maul has lent us another specimen taken off Madeira. Of the six specimens known to us, four are from the North Atlantic, and the other Eastern Pacific specimen is from off Colombia. The two Pacific specimens differ slightly from the Atlantic specimens, but all appear to be conspecific. The specimen taken with the *Cobb* trawl from about 305 km. (190 miles) SSW. off Point Conception, Calif., is the largest known.

GIGANTUROIDEA

GIGANTURIDAE

61. *Bathyleptus lisae* Walters.

Figures 20 and 25C.

86.92, C6303, (1) 182 mm.

This is one of the larger and better preserved specimens of this species that has been taken (V. Walters, personal communication). Alive when it came on deck in the trawl, it bit the junior author on the finger. Despite a number of trenchant morphological differences (that may have an ontogenetic basis), there are certain similarities between this species and *Rosaura rotunda* Tucker that suggest that they may have at least an intrasubordinal relationship.

LYOMERI

MONOGNATHIDAE

62. *Monognathus* sp.

60.140, H6204, (1) 51.5 mm.

This specimen, from about 630 km. (390 miles) WSW. of San Francisco, Calif., is probably one of the largest specimens of this little known group to be recorded; the intrageneric relationships are uncertain, and this specimen is therefore best not identified to species (G. L. Orton and R. H. Rosenblatt, personal communications).

FIGURE 19.—*Bathylaco nigricans*, 244 mm. SL, station 86.92, C6303.

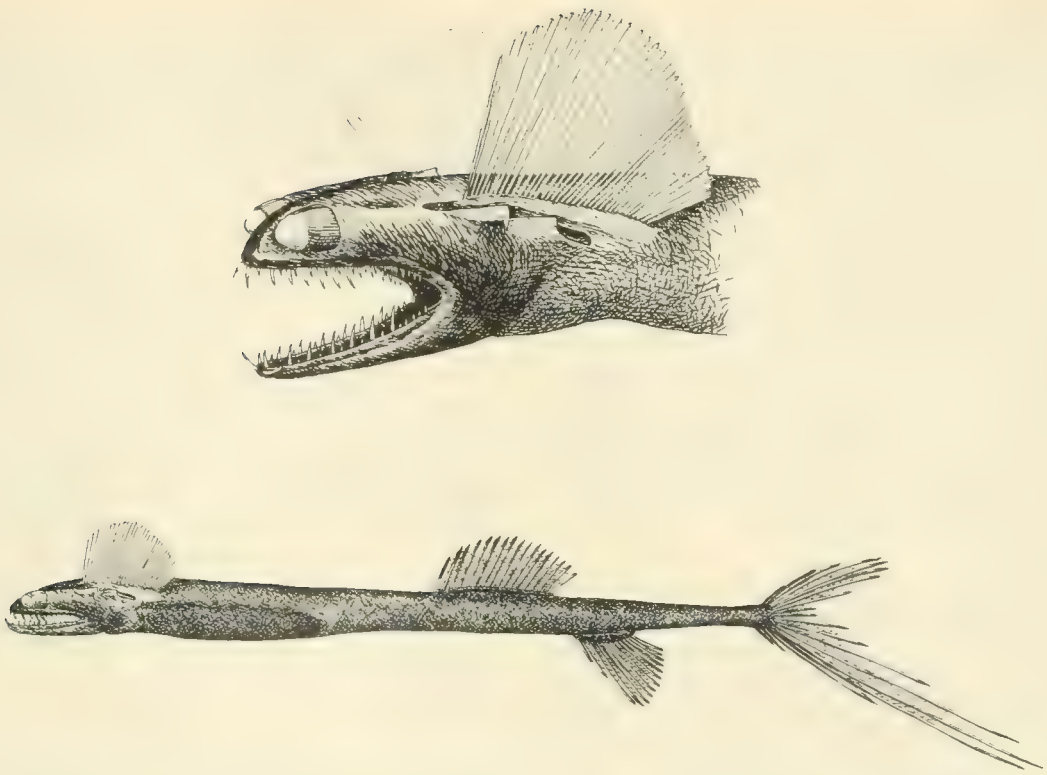

FIGURE 20.—*Bathyleptus lisae* (head and lateral views), 182 mm. SL, station 86.92, C6303.

CETUNCULI

CETOMIMIDAE

63. *Ditropichthys* sp.

90.200, H6204, (1) 38.5 mm.

This specimen, from about 1,000 km. (620 miles) WSW. off Point Conception, Calif., is identified as an undescribed species of *Ditropichthys* by R. R. Rofen (personal communication), who is preparing a detailed description for publication.

INIOMI

NEOSCOPELIDAE

64. *Scopelengys tristis* Alcock.

86.92, C6303, (1) 182 mm.; 90.45a, H6105, (2) 115–143 mm.; 120.50, H6204, (1) 103 mm.

These specimens were taken about 305 km. (190 miles) SE. of Point Conception, about 95 km. (60 miles) SE. of San Pedro, Calif., and about 70 km. (45 miles) W. of Punta Eugenia, Baja California.

MYCTOPHIDAE

65. *Hierops crockeri* (Bolin).

Figure 16C.

60.60, H6204, (1) 29 mm.; 60.70, H6204, (11) 24–35 mm.; 60.70, C6208, (7) 30–36.5 mm.; 60.80, H6204, (8) 22–39 mm.; 60.80, C6208, (2) 35–36 mm.; 60.90, H6204, (16) 15–40 mm.; 60.100, H6204, (3) 23–27 mm.; 60.100, C6208, (1) 38 mm.; 60.120, B6203, (4) 22–38 mm.; 60.120, H6204, (5) 34–38 mm.; 60.140, H6204, (3) 21.5–37 mm.; 60.160, H6204, (4) 34–39 mm.; 60.180, H6204, (1) 24 mm.; 60.200, B6203, (1) 30 mm.; 60.200, H6204, (1) 22 mm.; 70.60, C6208, (2) 22–37 mm.; 70.100, C6208, (2) 36–39 mm.; 80.60, C6208, (2) 23.5–38 mm.; 80.70, B6203, (1) 27 mm.; 80.70, H6204, (3) 10–27 mm.; 80.70, C6208, (1) 19 mm.; 80.75, B6303, (1) 15.3 mm.; 80.80, H6204, (6) 26–42 mm.; 80.100, H6204, (2) 15–16 mm.; 80.140, C6208, (4) 27–46 mm.; 80.150, C6208, (6) 30–52 mm.; 80.170, C6208, (2) 39–45 mm.; 80.180, C6208, (2) 39 mm.; 80.190, C6208, (1) 24 mm.; 80.200, C6208, (1) 45 mm.; 83.77, C6303, (26) 25–36 mm.; 83.90, C6303, (79) 25–39 mm.; 84.67, C6303, (11) 15–36 mm.; 84.68, C6303, (6) 26–35.5 mm.; 86.92, C6303, (4) 27.8–34.5 mm.; 87.80, C6303, (2) 19–28 mm.; 90.45, H6204, (1) 35.5 mm.; 90.48a, H6105, (1) 18.5 mm.; 90.48b, H6105, (5) 12.5–14 mm.; 90.60, C6208, (2) 26–28 mm.; 90.70, H6204, (2) 35–42 mm.; 90.100, C6208, (2) 19–23.5 mm.; 90.140, C6208, (2) 20–46 mm.;

90.160, C6208, (3) 31–40 mm.; 90.180, C6208, (3) 34–43 mm.; 90.200, C6208, (3) 33–40 mm.; 93.31, C6303, (1) 18.5 mm.; 94.32a, B6204, (1) 26 mm.; 97.40, C6303, (2) 17.5–21 mm.; 97.50, B6203, (2) 29–dis., mm.; 97.65, C6303, (4) 31–45 mm.; 100.60, H6204, (1) 25 mm.; 100.65, C6303, (6) 26.5–32.5 mm.; 100.80, H6204, (1) 17.5 mm.; 100.90, H6204, (1) 27.5 mm.; 100.120, H6204, (1) 49 mm.; 100.160, H6204, (1) 45 mm.; 103.50, C6303, (4) 20–23 mm.; 108.63, C6303, (2) 23–43.5 mm.; 110.100, H6204, (1) 15 mm.; 110.140, H6204, (2) 31–44 mm.; 110.160, H6204, (1) 45 mm.; 120.60, H6204, (5) 18.5–26 mm.; 120.70, H6204, (1) 43 mm.; 120.80, H6204, (12) 20–46 mm.; 120.90, M6204, (3) 29–32 mm.

66. *Electrona rissoi* (Cocco).

Figure 16C.

80.150, C6208, (1) 30 mm.; 84.92, B6303, (1) 43.5 mm.; 90.100, C6208, (1) 58.5 mm.; 100.65, C6303, (3) 44.5–45.5 mm.; 110.140, H6204, (1) 48 mm.

67. *Hygophum* sp.

Figure 16D.

60.180, H6204, (1) 43 mm.; 60.200a, B6203, (5) 33–44 mm.; 73.200, B6203, (1) 45 mm.; 80.160, C6208, (246) 19–52.5 mm.; 80.170, C6208, (11) 30–47 mm.; 80.190, C6208, (28) 43–52 mm.; 80.200, C6208, (8) 39–53 mm.; 83.77, C6303, (1) 34 mm.; 86.92, C6303, (1) 36 mm.; 90.80, C6208, (3) 41–44 mm.; 90.90, C6303, (2) 37.5–39.5 mm.; 90.100, C6208, (2) 42 mm.; 90.110, B6203, (1) 42 mm.; 90.120, C6208, (86) 32–51 mm.; 90.140, C6208, (1) 40 mm.; 90.150, C6208, (40) 35–49 mm.; 90.160, H6204, (1) 26 mm.; 90.160, C6208, (10) 33.5–52 mm.; 90.190, C6208, (26) 41–55 mm.; 90.200, H6204, (3) 16–32 mm.; 92.115, B6303, (6) 24.5–40 mm.; 100.65, C6303, (1) 21.5 mm.; 100.100, H6204, (2) 37–43 mm.; 100.140, H6204, (3) 27–43 mm.; 100.160, H6204, (1) 13 mm.; 120.80, H6204, (1) 59 mm.; 123.45, B6212, (1) 45 mm.; 127.45, B6212, (1) 31.5 mm.

Taxonomic differentiation of the species in this genus is not definitive or convincing. Fraser-Brunner (1949:1050) synonymized *H. atratum* (Garman) with *H. reinhardti* (Lütken). There are indications, from other studies, that these two species are distinct (E. H. Ahlstrom, personal communication). The above specimens appear to represent either one or both of the cited nominal species.

68. *Benthosema suborbitale* (Gilbert).

90.160, H6204, (1) 31 mm.

This specimen was taken about 740 km. (460 miles) SE. of Point Conception, Calif.

69. *Diogenichthys atlanticus* (Tåning).

Figure 21A.

60.80, H6204, (1) 19 mm.; 60.160, B6203, (2) 27 mm.; 60.180, H6204, (6) 15–24 mm.; 60.200a, B6203, (3) 19–26 mm.; 60.200b, B6203, (4) 19.5–23.5 mm.; 70.80b, B6203, (1) 20 mm.; 70.80–5N, B6203, (8) 15–25 mm.; 70.200, H6204, (6) 9–22 mm.; 73.200, B6203, (2) 23–26 mm.; 80.80, C6208, (1) 18 mm.; 80.90, B6203, (1) 23 mm.; 80.90–5N, B6203, (55) 18–25 mm.; 80.90, H6204, (4) 13–22 mm.; 80.160, C6208, (7) all ca. 16 mm.; 80.190, C6208, (4) 16.5–20.5 mm.; 84.92, C6303, (1) 22.5 mm.; 90.48a, H6105, (1) 23 mm.; 90.80, C6208, (5) 20–23 mm.; 90.110, C6303, (3) 21–23.5 mm.; 90.120, H6204, (2) 22 mm.; 90.150, C6208, (1) 23 mm.; 90.160, H6204, (3) all 15 mm.; 90.190, C6208, (1) 20 mm.; 90.200, H6204, (5) 12–16.5 mm.; 100.60, H6204, (2) 22.5–25 mm.; 100.65, C6303, (4) 19.6–23.6 mm.; 100.80, H6204, (3) all 20 mm.; 100.100, H6204, (4) 22–24.5 mm.; 100.140, H6204 (10) 15–23 mm.; 100.160, H6204, (3) all 13 mm.; 110.120, H6204, (1) 16 mm.; 110.160, H6204, (1) 14.5 mm.

The records of capture shown on the chart suggest that *D. atlanticus* is a northern species in this area and *D. laternatus* is a southern species. Records from other collections show that in waters farther offshore than sampled by the survey, the distribution of *D. atlanticus* extends southward at least to lat. 20° N.

70. *Diogenichthys laternatus* (Garman).

Figure 21A.

120.70, H6204, (3) 23.5–24 mm.; 120.80, H6204, (2) 22.5–25 mm.; 120.90, H6204, (6) 22–25 mm.; 127.45, B6212, (1) 14 mm.; 130.40, B6212, (5) 16–25 mm.; 133.35, B6212, (1) 18.5 mm.; 137.35, B6212, (2) 13–18 mm.; 137.50, B6203, (6) 14.5–26 mm.; 140.35, B6212, (16) 12.1–24 mm.

71. *Symbolophorus californiense* (Eigenmann and Eigenmann).

Figure 21B.

60.80, C6208, (4) 60–95 mm.; 60.120, B6203, (4) 29–90 mm.; 60.160, B6203, (1) 32 mm.; 60.160, H6204, (1) 95 mm.; 66.100, C6208, (12) 48–71 mm.; 70.60, C6208, (4) 55–74 mm.; 70.80–5N, B6203, (9) 45–67 mm.; 70.80, C6208, (167) 39–91 mm.; 70.100, C6208, (1) 70 mm.; 80.52, C6208, (1) 75 mm.; 80.55, H6204, (1) 90 mm.; 80.60, H6204, (1) 73 mm.; 80.60, C6208, (7) 71–86 mm.; 80.65, B6303, (12) 42–94 mm.; 80.70, C6208, (2) 78–81 mm.; 80.75, B6203, (6) 27–59 mm.; 80.80, H6204, (2) 52–67 mm.; 80.80, C6208, (6) 53–73 mm.; 80.90, B6203, (4) 43–76 mm.; 80.90–5N, B6203, (5) 25–59 mm.; 80.90, H6204, (4) 32–67 mm.; 80.100, B6203, (34) 44–94 mm.; 80.200, C6208, (1) 30.5 mm.; 82.69, C6303, (24) 37.5–90 mm.; 83.77, C6303, (124) 32.5–85 mm.; 83.70b, B6303, (16) 51–95 mm.; 83.90, C6303, (2) 56–66 mm.; 83.70, C6303, (7) 53–70.5 mm.; 84.67, C6303, (3) 56.5–65.5 mm.; 84.92, B6303, (10) 39.5–90 mm.; 84.70, C6303, (28) 48–75 mm.; 86.92, C6303, (1) 57 mm.; 87.80, C6303, (2) 52.5–55.5 mm.; 87.90, C6303, (5) 46.5–64.5 mm.; 90.48a, H6105, (3) 57–77 mm.; 90.60, H6204, (1) 65 mm.; 90.70, C6208, (2) 66–70 mm.; 90.80, C6208, (5) 40–63 mm.; 90.90, C6303, (1) 73 mm.; 90.120, C6208, (5) 28–29.5 mm.; 90.190, C6208, (1) 27 mm.; 91.39a,

C6208, (4) 37.5–67 mm.; 91.39b, C6208, (3) 65–77.5 mm.; 97.40, C6303, (11) 48–86 mm.; 97.50, B6203, (4) 54–70 mm.; 97.65, C6303, (24) 32.5–51.5 mm.; 100.40, H6204, (1) 51 mm.; 100.60, H6204, (2) 24–60 mm.; 100.65, C6303, (86) 28–87.5 mm.; 100.90, H6204, (1) 28 mm.; 100.120, H6204, (1) 24 mm.; 103.50, C6303, (1) 54 mm.; 107.60, C6303, (21) 47–66 mm.; 108.63, C6303, (6) 49.5–62.5 mm.; 110.50, B6203, (1) 46 mm.

This species has generally been known as *Myctophum californiense*. It was designated as the type species of the new genus *Symbolophorus* by Bolin and Wisner in Bolin (1959: 11).

72. *Myctophum nitidulum* Garman.

Figure 21B.

60.200a, B6203, (1) 65 mm.; 90.150, C6208, (2) 50–68 mm.; 90.200, H6204, (1) 19 mm.; 100.65, C6303, (13) 48–63 mm.; 108.63, C6303, (1) 70 mm.; 110.120, H6204, (2) 25 mm.; 123.50, B6203, (2) 26–36 mm.

This species was recently synonymized with *M. margaritatum* Gilbert, the name by which it has been more commonly known, and was distinguished from *M. affine* (Lütken) by Bolin (1959: 14).

73. *Gonichthys tenuiculus* (Garman).

130.40, B6212, (1) 28 mm.; 137.50, B6203, (1) 44 mm.

These specimens were taken about 70 km. (45 miles) SW. of Ballenas Bay and about 160 km. (100 miles) W. of Santa Maria Bay, Baja California.

74. *Tarletonbeania crenularis* (Jordan and Gilbert).

Figure 16D.

60.60, H6204, (8) 12–62 mm.; 60.60, C6208, (7) 38–59 mm.; 60.70, H6204, (6) 22–35 mm.; 60.70, C6208, (3) 43–64 mm.; 60.80, H6204, (8) 12.5–32 mm.; 60.80, C6208, (9) 29–54 mm.; 60.90, H6204, (4) 23–31 mm.; 60.90, C6208, (2) 17–36 mm.; 60.100, H6204, (4) 13–31 mm.; 60.100, C6208, (3) 15–29 mm.; 60.120, B6203, (2) 26–30 mm.; 60.180, H6204, (3) all 15 mm.; 65.54, C6208, (8) 37–74 mm.; 70.51, C6208, (1) 44 mm.; 70.60, C6208, (1) 17 mm.; 70.80–5N, B6203, (1) 24 mm.; 77.51, C6208, (3) 34.5–45 mm.; 80.52, C6208, (77) 34–80 mm.; 80.55, H6204, (1) 32 mm.; 80.60, B6203, (1) 31 mm.; 80.60, H6204, (2) 30–31 mm.; 80.60, C6208, (8) 34–60 mm.; 80.65, B6303, (7) 28–36.5 mm.; 80.70, C6208, (2) 19 mm.; 80.75, B6303, (1) 27 mm.; 80.80, C6208, (1) 26 mm.; 80.90–5N, B6203, (3) 27–29 mm.; 80.90, H6204, (3) 17–34 mm.; 80.100, B6203, (1) 36 mm.; 80.100, H6204, (1) 16.5 mm.; 83.69, C6303, (43) 32.5–68 mm.; 83.70a, B6303, (2) 23–28 mm.; 83.70b, B6303, (3) 30.5–32.5 mm.; 83.77, C6303, (2) 18–50 mm.; 83.90, C6303, (15) 19.5–30.5 mm.; 84.67, C6303, (29) 37.5–61 mm.; 84.70, C6303, (16) 37.5–66.5 mm.; 84.92, B6303, (3) 14–26 mm.; 90.35, B6203, (1) 43 mm.; 90.45a, H6105, (1) 14.5 mm.; 90.45, H6204, (1) 29 mm.; 90.48a, H6105, (7) 16–32.5 mm.; 90.48b, H6105, (1) 14.5 mm.; 90.60, H6204, (8) 33–48 mm.; 90.70, C6208, (1) 28 mm.

75. *Lobianchia gemellari* (Cocco).

Fig 21D.

90.160, C6208, (5) 50–53 mm.; 90.200, C6208, (1) 31 mm.; 100.160, H6204, (1) 57 mm.

This species was listed as *Diaphus* (*Hyperphotops*) *gemellari* (Cocco) by Fraser-Brunner (1949: 1066). It was reestablished as the type species of the genus *Lobianchia* Gatti by Bolin (1959: 18). Taken some 800 km. (500 miles) WSW. of San Diego, these records would appear to approach the limit of its eastward distribution in this latitude.

76. *Diaphus theta* Eigenmann and Eigenmann.

Figure 21C.

60.60, H6204, (27) 24–53 mm.; 60.60, C6208, (13) 37–42 mm.; 60.70, H6204, (251) 28–40 mm.; 60.70, C6208, (8) 34–45 mm.; 60.80, H6204, (11) 25–71 mm.; 60.80, C6208, (34) 34–54 mm.; 60.90, H6204, (9) 29–63 mm.; 60.90, C6208, (8) 37–41 mm.; 60.100, H6204, (6) 30–63 mm.; 60.100, C6208, (1) 41 mm.; 60.120, B6203, (5) 32–66 mm.; 60.120, H6204, (2) 30–47 mm.; 60.160, H6204, (1) 56 mm.; 70.51, C6208, (12) 37.5–57 mm.; 70.80b, B6203, (4) 33–64 mm.; 70.80–5N, B6203, (38) 24–41 mm.; 70.80, C6208, (15) 32–48 mm.; 70.90, B6203, (1) 32 mm.; 79.54, B6303, (3) 30–52 mm.; 80.52, C6208, (2) 36–40 mm.; 80.55, H6204, (2) 29–31 mm.; 80.60, B6203, (2) 32–34 mm.; 80.60, H6204, (5) 25–34 mm.; 80.60, C6208, (16) 33–54 mm.; 80.70, B6203, (1) 26 mm.; 80.70, H6204, (1) 33 mm.; 80.70, C6208, (5) 37–44 mm.; 80.75, B6303, (8) 26–59 mm.; 80.80, H6204, (5) 27–67 mm.; 80.80, C6208, (22) 15–60 mm.; 80.90, B6203, (1) 55 mm.; 80.90–5N, B6203, (6) 22–39 mm.; 80.90, H6204, (3) 26–50 mm.; 82.69, C6303, (15) 26–57.5 mm.; 83.70a, B6303, (17) 29–60 mm.; 83.70b, B6303, (2) 135–53 mm.; 83.77, C6303, (45) 24–51 mm.; 83.90, C6303, (63) 22–56.5 mm.; 83.70, C6303, (11) 27–57.5 mm.; 84.67, C6303, (206) 24–50 mm.; 84.68, C6303, (70) 26.5–41.5 mm.; 84.70, C6303, (74) 23–50 mm.; 84.92, B6303, (1) 30 mm.; 87.80, C6303, (1) 26.5 mm.; 88.105b, B6303, (6) 21–24.5 mm.; 90.32, B6203, (16) 24–34 mm.; 90.32, H6204, (2) 27–31 mm.; 90.45, H6204, (3) 35–53 mm.; 90.47, C6208, (13) 35–40 mm.; 90.48a, H6105, (3) 34–39 mm.; 93.31, C6303, (5) 21–28.5 mm.; 97.40, C6303, (6) 23–29 mm.; 97.50, B6203, (2) 26–58 mm.; 97.65, C6303, (1) 29 mm.; 100.65, C6303, (1) 23 mm.; 100.120, H6204, (1) 33 mm.; 100.160, H6204, (1) 30 mm. (specimen damaged, identification questionable).

77. *Diaphus fulgens* Brauer.

Figure 21C.

60.200a, B6203, (1) 36 mm.; 87.200, B6203, (1) 30 mm.; 90.150, C6208, (2) 42 mm.; 90.200, C6208, (1) 38 mm.; 110.160, H6204, (3) 28.5—43 mm.

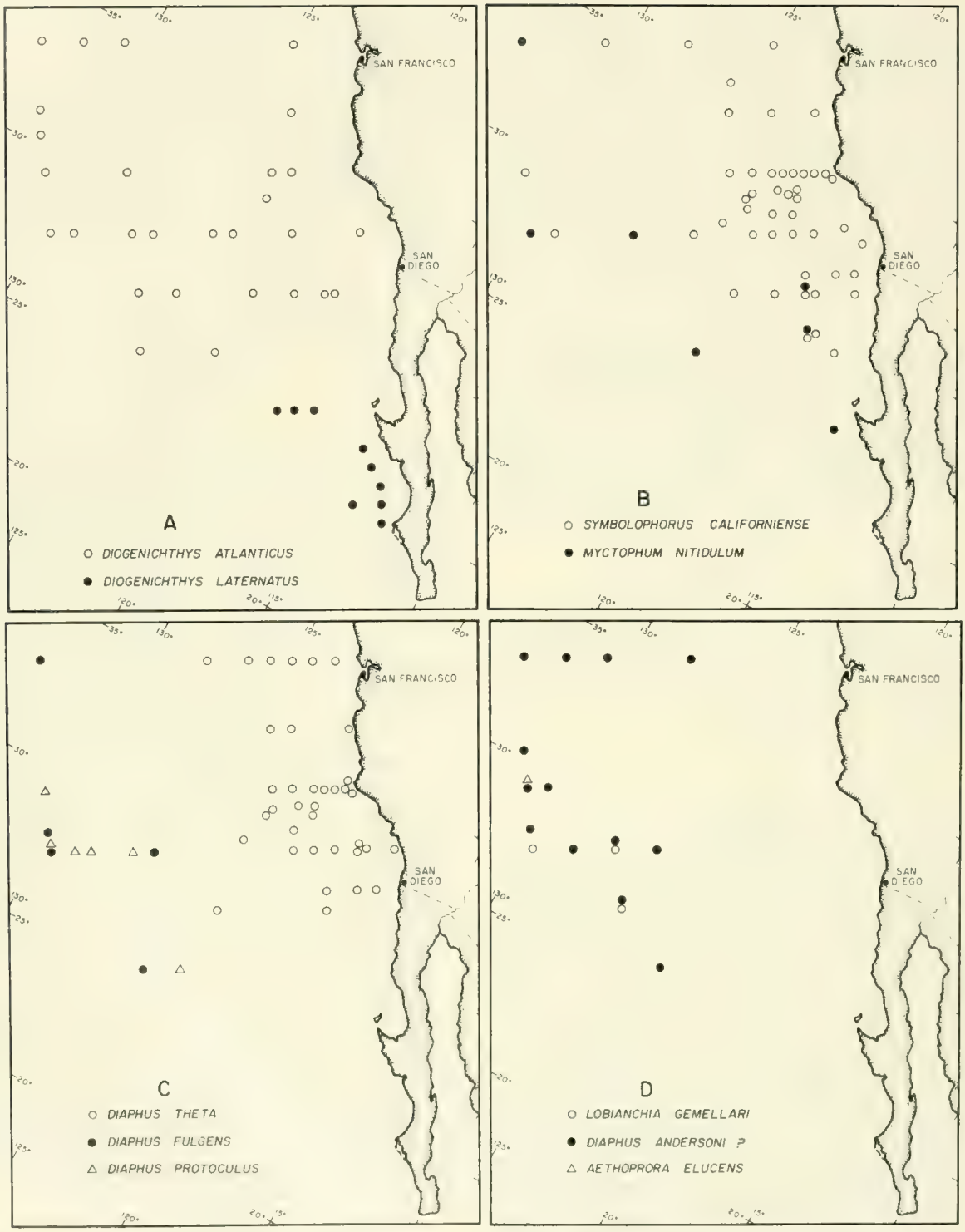

FIGURE 21.—Locations of capture of: A, *Diogenichthys atlanticus, Diogenichthys laternatus.* B, *Symbolophorus californiense, Myctophum nitidulum.* C. *Diaphus theta, Diaphus fulgens, Diaphus protoculus.* D. *Lobianchia gemellari, Diaphus andersoni?, Aethoprora elucens.*

These specimens and those of *D. protoculus* (following) were identified according to Fraser-Brunner (1949:1075). The differences between the two forms are slight, however, and *D. fulgens* may be a junior synonym of *D. protoculus*.

78. *Diaphus protoculus* Gilbert.

Figure 21C.

80.200, C6208, (1) 36.5 mm.; 90.160, C6208, (8) 31.5–43 mm.; 90.180, B6203, (1) 24 mm.; 90.190, C6208, (1) 37 mm.; 90.200, H6204, (1) 27 mm.; 110.140, H6204, (2) 43 mm.

79. *Diaphus andersoni* Tåning?

Figure 21D.

60.120, B6203, (21) 23–33 mm.; 60.120, H6204, (1) 30 mm.; 60.160, B6203, (1) 35 mm.; 60.180, H6204, (1) 25 mm.; 60.200, H6204, (1) 28 mm.; 73.200, B6203, (2) 25–28 mm.; 80.190, C6208, (1) 32 mm.; 80.200, C6208, (2) 26–29 mm.; 87.200, B6203, (1) 27 mm.; 90.140, C6208, (1) 27.5 mm.; 90.160, H6204, (1) 27 mm.; 90.160, C6208, (3) 26–30.5 mm.; 90.180, B6203, (3) 25–27 mm.; 90.180, H6204, (2) 29 mm.; 100.160, H6204, (3) 26.5–30.5 mm.; 110.140, H6204, (1) 30 mm.

D. andersoni had previously been recorded only from the South Pacific. The above specimens are obviously closely related to *D. andersoni*, but certain slight differences, especially the relative length of the luminous patch of tissue extending back from the lateral pectoral photophore (PLO), suggest that they may be distinct (R. L. Wisner, personal communication). If these differences warrant specific distinction of the above specimens from *D. andersoni*, then these specimens represent an undescribed species.

80. *Aethoprora elucens* (Brauer).

Figure 21D.

80.200, C6208, (1) 51 mm.

This species was listed as *Diaphus* (*Lamprossa*) *elucens* Brauer by Fraser-Brunner (1949: 1073). It was later placed in the genus *Aethoprora* Goode and Bean by Bolin (1959:22). This single record from about 970 km. (600 miles) off Point Conception undoubtedly represents a rare occurrence of the species off California.

81. *Notolychnus valdiviae* (Brauer).

Figure 22A.

60.180, H6204, (4) 20–24 mm.; 60.200a, B6203, (14) all ca. 14 mm.; 60.200, H6204, (3) 22–24 mm.; 70.200, H6204, (11) 17–25 mm.; 73.200, B6203, (67) 14–26 mm.; 80.200, C6208, (1) 22.5 mm.; 84.92, B6303, (2) 22–25 mm.; 87.200, B6203, (9) 18–26 mm.; 90.120, C6208, (2) 14.5–18.5 mm.; 90.160, H6204, (9) 18–25 mm.; 90.180, H6204, (2) 24–26 mm.; 90.200, H6204, (7) 20–24 mm.; 100.60, H6204, (1) 19 mm.; 100.80, H6204, (2) 23 mm.; 100.100, H6204, (1) 22 mm.; 100.140, H6204, (20) 19.5–24.5 mm.; 100.160, H6204, (24) 13–24 mm.; 110.160, H6204, (16) 20–30 mm.

82. *Lampadena urophaos* Paxton.

Figure 22B.

60.160, H6204, (1) 57 mm.; 86.92, C6303, (1) 50 mm.; 100.40, H6204, (1) 103 mm.

These specimens extend northward and seaward, the known range of this species recently described by Paxton (1963:29–33).

83. *Taaningichthys bathyphilus* (Tåning).

Figure 22B.

120.70, H6204, (1) 66.5 mm.

This species, previously known as *Lampadena bathyphila*, was designated as the type species of the new genus *Taaningichthys* by Bolin (1959: 25).

84. *Taaningichthys minimus* (Tåning).

Figure 22B.

80.200, C6208, (1) 52 mm.; 100.140, H6204, (1) 55 mm.

This species, formerly known as *Lampadena minima*, was one of the two species included in the new genus *Taaningichthys* described by Bolin (1959: 25). *T. minimus* was described from the North Atlantic Ocean—we know of no previous records of it from the Pacific Ocean.

85. *Taaningichthys* spp.

Figure 22B.

60.60, H6204, (1) 90 mm.; 60.140, H6204, (2) 80–85 mm.; 80.90, H6204, (1) 30 mm.; 100.60, H6204, (1) 70 mm.; 100.80, H6204, (1) 83 mm.; 110.160, H6204, (1) 51 mm.

The above six station records include more than one species of *Taaningichthys*. They are not, so far as known, *T. bathyphilus* or *T. minimus*, the only two species ascribed to this genus by Bolin (1959:25). Some of the above specimens lack photophores, and all of them may represent undescribed species.

86. *Stenobrachius leucopsarus* (Eigenmann and Eigenmann).

Figure 22A.

60.60, H6204, (95) 19–70 mm.; 60.70, H6204, (4) 20–26 mm.; 60.80, H6204, (20) 15.5–82 mm.; 60.80, C6208, (26) 25–63 mm.; 60.90, H6204, (10) 29–56 mm.; 60.90, C6208, (1) 51 mm.; 60.100, H6204, (1) 35 mm.; 60.120, H6204, (1) 38 mm.; 70.80b, B6203, (4) 33–64 mm.; 70.80–5N, B6203, (57) 26–60 mm.; 77.51, C6208, (6) 50–66 mm.; 79.54, B6303,

(8) 35.5–53 mm.; 80.52, C6208, (3) 49–52 mm.; 80.55, H6204, (117) 32–82 mm.; 80.60, B6203, (13) 33–57 mm.; 80.60, H6204, (154) 30–75 mm.; 80.60, C6208, (735) 22.5–78 mm.; 80.65, B6303, (4) 28–69 mm.; 80.70, H6204, (3) 36–71 mm.; 80.70, C6208, (24) 43–70 mm.; 80.75, B6303, (4) 34.5–71.5 mm.; 80.80, H6204, (8) 34–78 mm.; 80.90, B6203, (5) 38–60 mm.; 80.90–5N, B6203, (11) 31–51 mm.; 80.90, H6204, (4) 17–35 mm.; 80.100, B6203, (2) 32–36 mm.; 82.69, C6303, (38) 29–68.5 mm.; 83.70, C6303, (44) 49–72 mm.; 83.70a, B6303, (4) 57–59 mm.; 83.70b, B6303, (1) 29 mm.; 83.77, C6303, (29) 31–73 mm.; 83.90, C6303, (3) 38–62.5 mm.; 84.67, C6303, (43) 44–71 mm.; 84.70, C6303, (143) 31–74 mm.; 84.92, B6303, (4) 55–70 mm.; 90.32, B6203, (27) 29–72 mm.; 90.32, H6204, (21) 32–80 mm.; 90.45, H6105, (51) 37–78 mm.; 90.47, C6208, (74) 44–72 mm.; 90.48a, H6105, (135) 10.5–74 mm.; 90.48b, H6105, (4) 10–17.5 mm., 90.60, H6204, (257) 30–65 mm.; 90.70, H6204, (1) 38 mm.; 90.70, C6208, (10) 42–63 mm.; 93.29, C6208, (1) adult; 94.32a, B6204, (4) 36–69 mm.; 94.32b, B6204, (7) 52–67 mm.; 95.31a, B6204, (8) 33–49 mm.; 95.31b, B6204, (11) 35–66 mm.; 95.31c, B6204, (20) 34–59 mm.; 97.40, C6303, (67) 32–76 mm.; 97.50, B6203, (1) 51 mm.; 97.65, C6303, (3) 50–63 mm.; 100.40, H6204, (12) 39–72 mm.; 100.65, C6303, (12) 49.5–62 mm.

This species has usually been recorded as *Lampanyctus leucopsarus*, although it was recorded as *Lampanyctus* (*Stenobrachius*) *leucopsarus* by Fraser-Brunner (1949:1082). *Stenobrachius* is distinctive enough to warrant full generic status (R. L. Wisner, personal communication).

87. *Lampanyctus* (*Triphoturus*) *mexicanus* (Gilbert).

Figure 22C.

60.60, H6204, (1) 35 mm.; 80.55, H6204, (2) 34–55 mm.; 80.60, H6204, (3) 35–47 mm.; 80.65, B6303, (1) 23 mm.; 80.70, H6204, (4) 28–57 mm.; 80.75, B6303, (1) 24.5 mm.; 80.80, H6204, (3) 27–62 mm.; 80.80, C6208, (2) 37–43 mm.; 80.90–5N, B6203, (13) 26–58 mm.; 80.90, H6204, (12) 24–60 mm.; 80.100, B6203, (1) 48 mm.; 82.69, C6303, (29) 22–61.5 mm.; 83.70a, B6303, (1) 23.5 mm.; 83.70b, B6303, (3) 28–29 mm.; 83.77, C6303, (84) 24–67.5 mm.; 84.67, C6303, (1) 44 mm.; 84.92, B6303, (1) 50 mm.; 86.92, C6303, (93) 44–67 mm.; 87.80, C6303, (58) 38.5–66.5 mm.; 87.90, C6303, (1) 43.5 mm.; 90.32, B6203, (10) 32–58 mm.; 90.32, H6204, (11) 28–49 mm.; 90.45, H6105, (35) 29–54 mm.; 90.45, H6204, (1) 29 mm.; 90.47, C6208, (3) 42–60 mm.; 90.48a, H6105, (79) 14–66 mm.; 90.60, B6203, (1) 24 mm.; 90.60, H6204, (10) 30–59 mm.; 90.70, C6208, (2) 47–54 mm.; 90.120, H6204, (1) 27 mm.; 90.160, H6204, (1) 56 mm.; 91.39a, C6208, (1) 43 mm.; 93.100, C6303, (3000) 25–70 mm.; 94.32a, B6204, (14) 30–57 mm.; 95.31b, B6204, (2) 31–34 mm.; 97.40, C6303, (715) 23–66 mm.; 97.50, B6203, (5) 29–57 mm.; 97.65, C6303, (20) 26–66 mm.; 100.40, H6204, (20) 38–65 mm.; 100.40, C6303, (2) 54 mm.; 100.50, H6204, (1) 60 mm.; 100.60, H6204, (22) 30–66 mm.; 100.65, C6303, (461) 22.5–67 mm.; 100.80, H6204, (3) 27–60 mm.; 100.90, H6204, (17) 52–71 mm.; 100.100, H6204, (7) 23–63 mm.; 100.120, H6204, (1) 58 mm.; 100.140, H6204, (5) 31.5–58.5 mm.; 107.60, C6303, (1) 37 mm.; 108.63, C6303, (1857) 24–72 mm.; 110.35, H6204, (11) 35–66 mm.; 110.40, H6204, (83) 28.5–70 mm.; 110.46, C6303, (2) 47.5 mm.; 110.50, B6203, (22) 23–69 mm.; 110.120, H6204, (13) 24–67 mm.; 110.160, H6204, (1) 28 mm.; 111.36a, C6303, (ca. 600) adults and juveniles; 111.37b, C6303, (101) 32–62 mm.; 113.34a, C6303, (29) 25–60 mm.; 118.43, B6212, (613) 16.5–43 mm.; 120.45, H6204, (307) 22–69 mm.; 120.45, B6212, (22) 16.5–56 mm.; 120.50, H6204, (299) 26–68 mm.; 120.60, H6204, (2) 23.5–24 mm.; 120.70, H6204, (33) 25.5–64 mm.; 120.80, H6204, (83) 26.5–66 mm.; 120.90, H6204, (28) 27–65 mm.; 123.45, B6212, (98) 15.5–56 mm.; 123.50, B6203, (135) 23–70 mm.; 127.45, B6212, (48) 17.5–60.5 mm.; 130.40, B6212, (40) 18–56.5 mm.; 133.35, B6212, (20) 17.5–40 mm.; 137.35, B6212, (6) all 20 mm.; 137.50, B6203, (5) 25–59 mm.; 140.35, B6212, (183) 16.5–53 mm.

88. *Lampanyctus* (*Triphoturus*) *nigrescens* Brauer.

Figure 22C.

60.180, H6204, (1) 25 mm.; 60.200, H6204, (1) 28 mm.; 70.200, H6204, (2) 26 mm. and damaged adult; 80.160, C6208, (3) 30–33 mm.; 87.200, C6208, (2) 32–38 mm.; 90.160, C6208, (1) 31 mm.

89. *Lampanyctus* (*Triphoturus*) *microchir* Gilbert.

Figure 22C.

80.200, C6208, (1) 35 mm.

90. *Lampanyctus ritteri* Gilbert.

Figure 22D.

60.60, H6204, (6) 38–84 mm.; 60.80, H6204, (9) 30–83 mm.; 60.80, C6208, (35) 43–88 mm.; 60.90, H6204, (5) 35–98mm.; 60.90, C6208, (2) 42–51 mm.; 60.100, H6204, (6) 29–67 mm.; 60.120, B6203, (13) 28–92 mm.; 60.120, H6204, (12) 43–115 mm.; 60.140, H6204, (8) 20–105 mm.; 60.160, H6204, (4) 36–118 mm.; 70.80b, B6203, (7) 39–44 mm.; 70.80–5N, B6203, (120) 28–57 mm.; 73.200, B6203, (1) 25 mm.; 80.55, H6204, (8) 40–104 mm.; 80.60, B6203, (7) 22–64 mm.; 80.60, H6204, (20) 36–105 mm.; 80.60, C6208, (42) 33–80 mm.; 80.70, H6204, (10) 44–115 mm.; 80.75, B6303, (8) 34–76.5 mm.; 80.80, H6204, (35) 35–109 mm.; 80.90, B6203, (5) 38–60 mm.; 80.90–5N, B6203, (4) 37–44 mm.; 80.90, H6204, (27) 26–96 mm.; 80.100, B6203, (14) 28–70 mm.; 82.69, C6303, (121) 30–84 mm.; 83.70, C6303, (3) 49–72.5 mm.; 83.70a, B6303, (5) 43.5–70 mm.; 83.77, C6303, (259) 28.5–90 mm.; 83.90, C6303, (1) 66 mm.; 84.67, C6303, (36) 31–65.5 mm.; 84.70, C6303, (6) 37–95 mm.; 84.92, B6303, (31) 23–93 mm.; 86.92, C6303, (31) 38–110 mm.; 87.80, C6303, (8) 34–78 mm.; 90.32, B6203, (8) 36–60 mm.; 90.32, H6204, (1) 47 mm.; 90.45a, H6105, (2) 47–107 mm.; 90.47, C6208, (2) 51–73 mm.; 90.48a, H6105, (120) 23.5–97 mm.; 90.60, B6203, (2) 48 mm.; 90.60, H6204, (60) 35–106 mm.; 90.70, H6204, (20) 39–112 mm.; 90.70, C6208, (14) 27.5–70 mm.; 91.39a, C6208, (1) 54 mm.; 93.100, C6303, (8) 82–93 mm.; 94.32a, B6204, (1) 95 mm.; 94.32b, B6204, (2) 66–82 mm.; 97.40, C6303, (88)

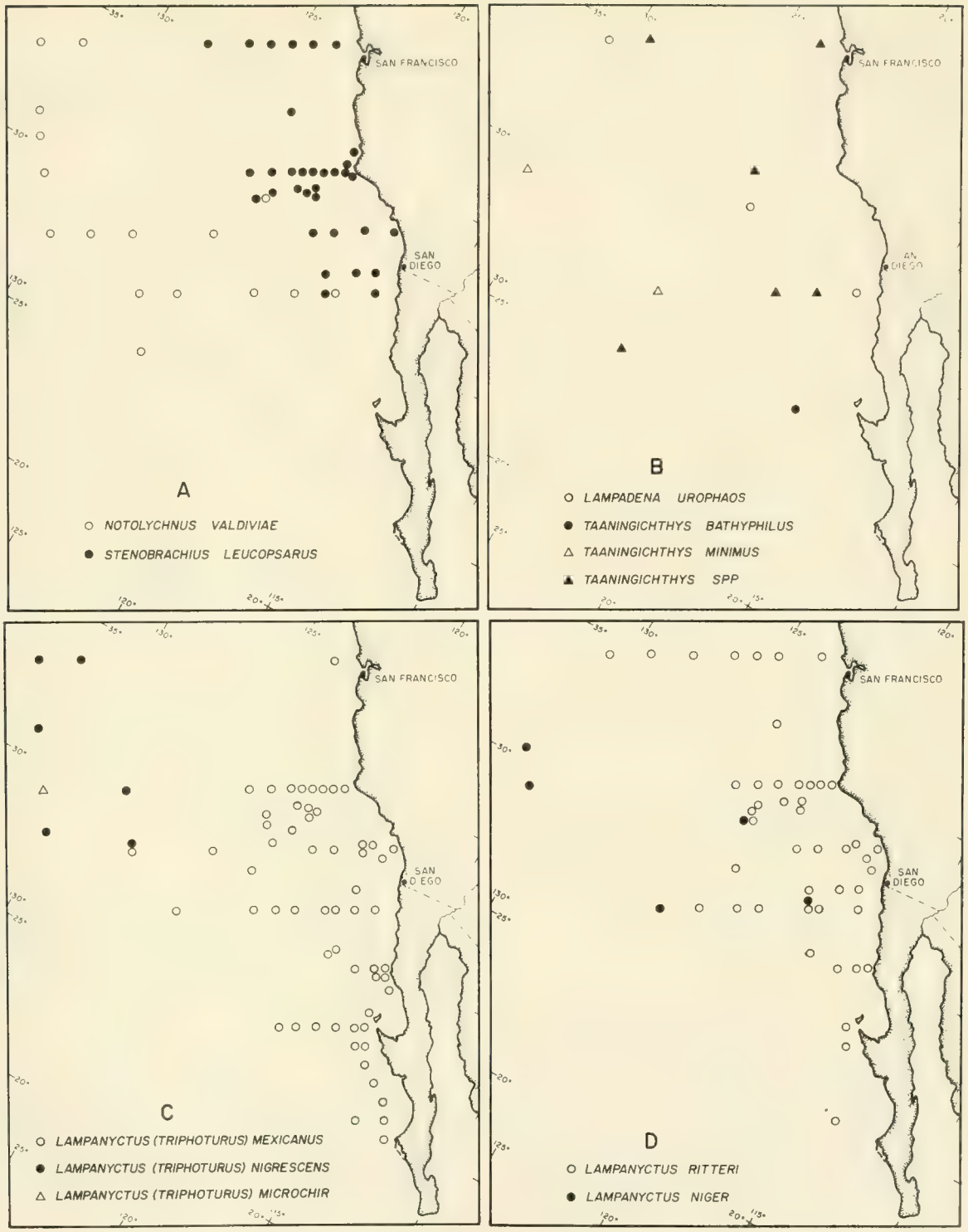

FIGURE 22.—Locations of capture of: A, *Notolychnus valdiviae, Stenobrachius leucopsarus.* B, *Lampadena urophaos, Taaningichthys bathyphilus, Taaningichthy sminimus, Taaningichthys spp,* C. *Lampanyctus (Triphoturus) mexicanus, Lampanyctus (Triphoturus) nigrescens, Lampanyctus (Triphoturus) microchir.* D, *Lampanyctus ritteri, Lampanyctus niger.*

28–108 mm.; 97.50, B6203, (7) 32–97 mm.; 97.65, C6303, (2) 46 mm.; 100.40, H6204, (12) 48–97 mm.; 100.60, H6204, (6) 28–110 mm.; 100.65, C6303, (47) 27.5–99.5 mm.; 100.90, H6204, (1) 107 mm.; 100.100, H6204, (1) 24.5 mm.; 100.120, H6204; (1) 84 mm.; 108.63, C6303, (15) 28–99 mm.; 110.35, H6204, (1) 30 mm.; 110.40, H6204, (3) 88–105 mm.; 110.50, B6203, (2) 46–90 mm.; 120.45, H6204, (2) 35–115 mm.; 123.50, B6203, (1) 27 mm.; 137.50, B6203, (2) 43 mm.

91. *Lampanyctus regalis* (Gilbert).

Figure 23A.

60.60, H6204, (3) 57–76 mm.; 60.80, C6208, (1) 64 mm.; 60.90, H6204, (2) 50–58 mm.; 60.100, H6204, (1) 36 mm.; 60.120, B6203, (1) 38 mm.; 60.180, H6204, (2) 24–25 mm.; 70.200, H6204, (1) 4.5 mm.; 80.55, H6204, (3) 41–53 mm.; 80.60, B6203, (1) 40 mm.; 80.60, H6204, (2) 42–44 mm.; 80.75, B6303, (2) 27.5–39.5 mm.; 83.69, C6303, (1) 36 mm.; 83.77, C6303, (1) 39 mm.; 84.67, C6203, (1) 43 mm.; 87.200, B6203, (2) 34–35 mm.; 90.32, H6204, (1) 43 mm.; 90.45a, H6105, (2) 48–52 mm.; 90.60, H6203, (1) 35 mm.; 90.160, H6204, (3) 38–49 mm.; 97.50, B6203, (2) 44 mm.; 100.65, C6303, (2) 36–48 mm.; 100.120, H6204, (1) 39 mm.

92. *Lampanyctus idostigma* Parr.

Figure 23A.

120.80, H6204, (1) 44 mm.; 120.90, H6204, (3) 30–59 mm.

93. *Lampanyctus niger* Günther.

Figure 22D.

73.200, B6203, (1) 36 mm.; 80.200, C6208, (1) 42 mm.; 86.92, C6303, (7) 51–88 mm.; 100.65, C6303, (1) 62 mm.; 100.140, H6204, (2) 111 mm.

94. *Lampanyctus niger* Günther?

60.180, H6204, (1) 64 mm.; 87.80, C6303, (2) 72–89 mm.; 100.100, H6204, (1) 44.5 mm.; 100.160, H6204, (1) 102 mm.

These damaged specimens appear to represent this species, but their identity is uncertain.

95. *Lampanyctus steinbecki* Bolin.

Figure 23B.

60.140, H6204, (1) 54 mm.; 60.160, H6204, (1) 77 mm.; 60.180, H6204, (3) 37.5–47.5 mm.; 60.200a, B6203, (2) 39 mm.;60.200, H6204, (3) 28–112 mm.; 70.200, H6204, (7) 26–53 mm.; 73.200, B6203, (6) 25–42 mm.; 80.200, C6208, (1) 40 mm.; 83.77, C6303, (1) 30.5 mm.; 87.80, C6303, (1) 35.2 mm.; 90.160, H6204, (1) 43.5 mm.; 90.160, C6208, (2) 35–41 mm.; 90.180, B6203, (1) 39 mm.; 90.180, H6204, (12) 35–47 mm.; 90.200, H6204, (3) 28–33 mm.; 100.140, H6204, (3) 25–37 mm.; 110.160, H6204, (6) 23–51 mm.

96. *Lampanyctus tenuiformes* (Brauer).

Figure 23B.

83.77, C6303, (1) 38 mm.; 100.65, C6303, (2) 34–35 mm.

97. *Lampanyctus parvicauda* Parr.

Figure 23B.

137.50, B6203, (1) 60 mm.

This species was distinguished from the closely related *L. omostigma* Gilbert by Wisner (1963: 16–23.)

98. *Lampanyctus* sp. (no pectorals).

Figure 23B.

60.180, H6204, (1) 63 mm.; 60.200, B6203, (3) 30–65 mm.; 60.200, H6204, (3) 56–60 mm.; 70.200, H6204, (2) 23–39 mm.; 73.200, B6203, (3) 57–66 mm.; 80.80, H6204, (1) 61 mm.; 80.100, B6203, (1) 62 mm.; 80.200, C6208, (4) 31.5–62 mm.; 83.77, C6303, (1) 32 mm.; 86.92, C6303, (10) 47.5–60 mm.; 87.80, C6303, (1) damaged adult; 90.32, H6204, (1) 46 mm.; 90.48a, H6105, (1) 30 mm.; 90.70, C6208, (1) 48 mm.; 90.160, H6204, (4) 26–64 mm.; 90.160, C6208, (12) 45–58 mm.; 90.180, H6204, (10) 27–68 mm.; 90.200, H6204, (2) 59–63 mm.; 100.60, H6204, (2) 25–32 mm.; 100.90, H6204, (1) 35 mm.; 100.120, H6204, (1) 55 mm.; 100.140, H6204, (7) 25.5–59 mm.; 100.160, H6204, (4) 49–60 mm.; 110.120, H6204, (1) 50 mm.; 120.90, H6204, (1) 47 mm.

These specimens probably represent an undescribed species. None of them possesses visible pectoral fins, and cleared and stained specimens have no pectoral fin ray bases or actinosts and fewer vertebrae than are usually found in the genus *Lampanyctus*. Pattern and numbers of photophores also reveal certain differences between this form and other members of the genus. They are specifically distinct from the pectoral-less *Lampanyctus achirus* described as a new species by Andriashev (1962: 257–259).

99. *Lampanyctus* sp.

110.160, H6204, (1) 22 mm.

This single specimen, from about 800 km. (500 miles) westward of Punta Eugenia, Baja California, probably represents an undescribed species (R.L. Wisner, personal comunication).

100. *Lampanyctus* spp., unidentified.

60.100, H6204, (1) head only; 84.68, C6303, (1) juvenile; 84.92, B6303, (2) juvenile and adult; 90.70, H6204, (3) 52–90 mm.; 90.160, H6204, (1) 20 mm.; 90.190, C6208, (1) 40 mm.; 90.200, H6204, (2) larva and juvenile; 100.50, H6204, (1) 67 mm.; 100.160, H6204, (3) juveniles; 110.35, H6204, (1) 37 mm.; 110.140, H6204, (5) juveniles; 137.50, B6203, (4) 30–35 mm.

These specimens probably represent several species, but they are either too damaged or too immature to allow specific identification without adequate comparative material.

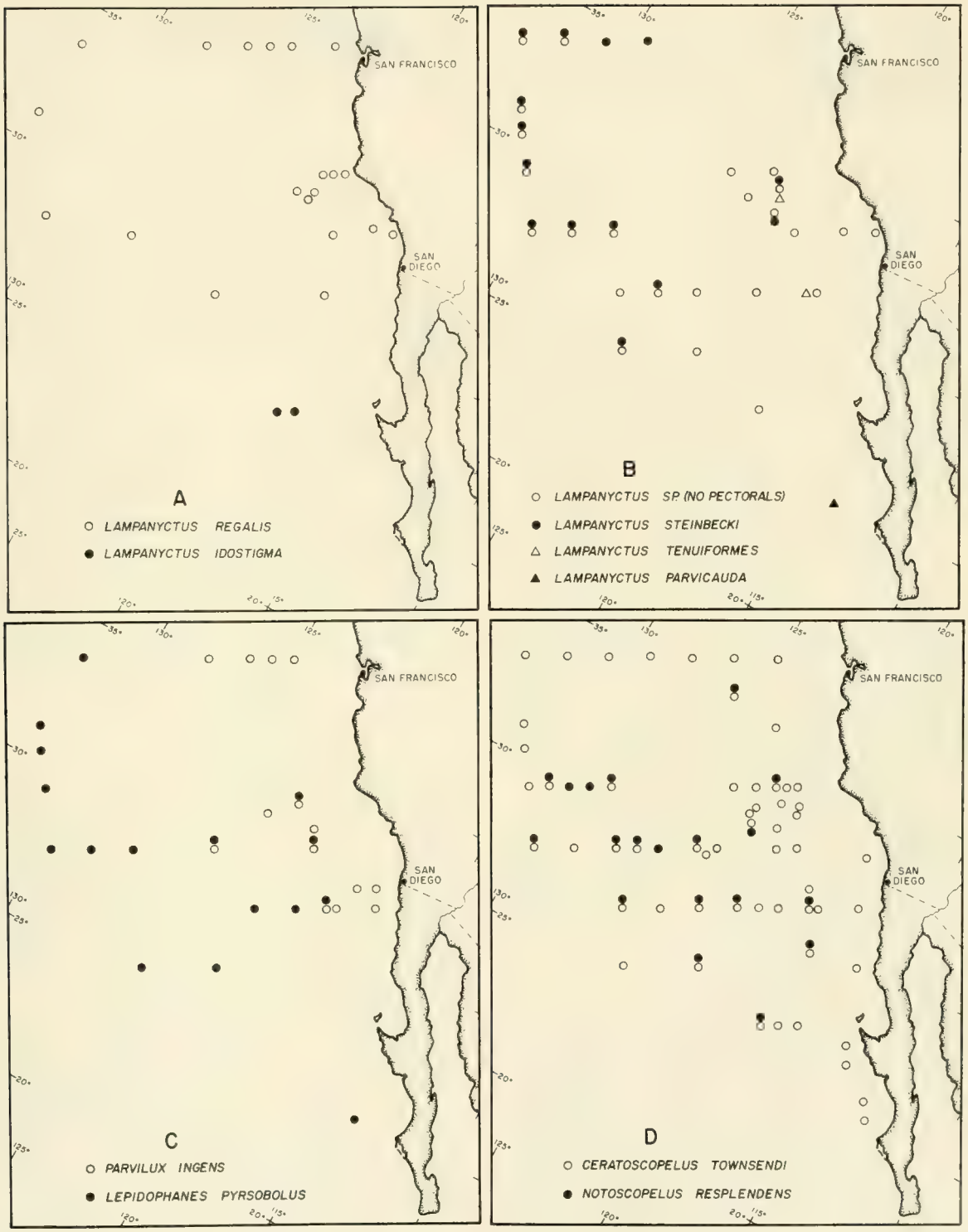

FIGURE 23.—Locations of capture of: A, *Lampanyctus regalis, Lampanyctus idostigma.* B, *Lampanyctus* sp. (no pectorals), *Lampanyctus steinbecki, Lampanyctus tenuiformes, Lampanyctus parvicauda.* C, *Parvilux ingens, Lepidophanes pyrsobolus.* D, *Ceratoscopelus townsendi, Notoscopelus resplendens.*

101. *Parvilux ingens* Hubbs and Wisner.

Figure 23C.

60.80, C6208, (3) 108–128 mm.; 60.90, H6204, (1) 95 mm.; 60.100, H6204, (1) 74 mm.; 60.120, H6204, (2) 56–96 mm.; 83.77, C6303, (1) 51.5 mm.; 86.92, C6303, (6) 93–178 mm.; 87.80, C6303, (1) 174 mm.; 90.70, C6208, (2) 134–157 mm.; 90.120, H6204, (1) 121 mm.; 97.40, C6303, (2) 52 mm.; 97.50, B6203, (2) 74–76 mm.; 100.40, H6204, (1) 72 mm.; 100.60, H6204, (1) 76 mm.; 100.65, C6303, (4) 139–192 mm.; 110.46, C6303, (1) 166 mm.

102. *Lepidophanes pyrsobolus* (Alcock).

Figure 23C.

60.180, H6204, (1) 25 mm.; 70.200, H6204, (1) 42 mm.; 73.200, B6203, (4) 21–30 mm.; 80.200, C6208, (1) 33.5 mm.; 83.77, C6303, (6) 29.5–42 mm.; 90.70, C6208, (2) 36 mm.; 90.120, H6204, (2) 31–37 mm.; 90.160, H6204, (3) 22–38 mm.; 90.160, C6208, (8) 29–40 mm.; 90.180, H6204, (1) 38 mm.; 90.200, H6204, (2) 30–34 mm.; 100.65, C6303, (6) 30.5–45.5 mm.; 100.80, H6204, (1) 30 mm.; 100.100, H6204, (3) 29.5–31.5 mm.; 100.140, H6204, (5) 22.5–46 mm.; 110.120, H6204, (2) 24–28 mm.; 110.160, H6204, (5) 23–44 mm.; 137.50, B6203, (1) 27 mm.

103. *Ceratoscopelus townsendi* (Eigenmann and Eigenmann).

Figure 23D.

60.80, H6204, (3) 33–55 mm.; 60.100, H6204, (6) 35–60 mm.; 60.120, B6203, (2) 40–56 mm.; 60.120, H6204, (1) 43 mm.; 60.140, H6204, (2) 53 mm.; 60.160, H6204, (2) 72–83 mm.; 60.180, H6204, (2) 31–32 mm.; 60.200, B6203, (1) 25 mm.; 66.100, C6208, (7) 23–35 mm.; 70.80b, B6203, (2) 29–38 mm.; 70.80–5N, B6203, (35) 22–52 mm.; 70.200, H6204, (3) 13–44 mm.; 73.200, B6203, (1) 52 mm.; 80.70, H6204, (1) 52 mm.; 80.75, B6303, (1) 52 mm.; 80.80, H6204, (3) 22–52 mm.; 80.90–5N, B6203, (66) 29–55 mm.; 80.90, H6204, (15) 40–59 mm.; 80.100, B6203, (1) 54 mm.; 80.160, C6208, (1) 22.5 mm.; 80.190, C6208, (1) 24 mm.; 80.200, C6208, (11) 19–56 mm.; 82.69, C6303, (24) 33.5–57.5 mm.; 83.77, C6303, (716) 33.5–61 mm.; 83.90, C6303, (142) 33–51 mm.; 84.67, C6303, (11) 40–50 mm.; 84.70, C6303, (1) 44 mm.; 84.92, B6303, (4) 29.5–57 mm.; 86.92, C6303, (11) 33.5–52.5 mm.; 87.80, C6303, (6) 36–47.5 mm.; 90.48a, H6105, (1) 42 mm.; 90.70, H6204, (2) 45–48 mm.; 90.80, C6208, (5) 23–32 mm.; 90.110, C6303, (1) 25.5 mm.; 90.120, H6204, (4) 18–49 mm.; 90.120, C6208, (64) 19–26.5 mm.; 90.150, C6208, (73) 15–27 mm.; 90.160, H6204, (5) 19–50 mm.; 90.160, C6208, (6) 48–53 mm.; 90.180, B6203, (1) 21 mm.; 90.180, H6204, (6) 29–57 mm.; 90.180, C6208, (1) 21 mm.; 90.200, H6204, (9) 15–53 mm.; 91.39a, C6208, (1) 52 mm.; 92.115, B6303, (1) 24 mm.; 97.40, C6303, (7) 38–51 mm.; 97.65, C6303, (85) 28.5–44 mm.; 100.60, H6204, (9) 38–51 mm.; 100.65, C6303, (944) 20–52 mm.; 100.80, H6204, (2) 36–40 mm.; 100.90, H6204, (1) 38 mm.; 100.100, H6204, (9) 22.5–59 mm.; 100.120, H6204, (3) 47–50 mm.; 100.140, H6204, (9) 20–29 mm.; 100.160, H6204, (2) 21–39 mm.; 108.63, C6303, (118) 29.5–46.5 mm.; 110.40, H6204, (1) 40 mm.; 110.120, H6204, (3) 24–30 mm.; 110.160, H6204, (13) 17–54 mm.; 120.70, H6204, (8) 30–41 mm.; 120.80, H6204, (9) 26.5–46 mm.; 120.90, H6204, (9) 25–39 mm.; 123.45, B6212, (6) 24–29.5 mm.; 127.45, B6212, (1) 22.5 mm.; 133.35, B6212, (1) 20.5 mm.; 140.35, B6212, (1) 32.5 mm.

104. *Notoscopelus resplendens* Richardson.

Figure 23D.

66.100, C6208, (3) 29–37 mm.; 80.80, H6204, (1) 58 mm.; 80.160, C6208, (2) 27 mm.; 80.170, C6208, (1) 31 mm.; 80.190, C6208, (3) 27.5–31 mm.; 86.92, C6303, (3) 56.2–60.5 mm.; 90.120, C6208, (15) 26–31 mm.; 90.140, C6208, (1) 27 mm.; 90.150, C6208, (12) 22.5–32.5 mm.; 90.160, H6204, (1) 64 mm.; 90.200, H6204, (1) 15 mm.; 100.65, C6303, (18) 43–64 mm.; 100.100, H6204, (1) 34.5 mm.; 100.120, H6204, (1) 70 mm.; 100.160, H6204, (1) 26 mm.; 108.63, C6303, (2) 44–60 mm.; 110.120, H6204, (1) 61 mm.; 120.90, H6204, (1) 67 mm.

105. Myctophidae, unidentified.

60.55, C6280, (1) discarded at sea; 70.80–5N, B6203, (1) adult; 70.200, H6204, (1) juvenile; 80.80, C6303, (2) discarded at sea; 80.90, B6203, (4) adults; 90.140, C6208, (2) juveniles; 90.150, C6208, (1) adult; 90.160, H6204, (2) juveniles; 90.200, H6204, (2) larvae, may be *Lepidophanes pyrosobolus*.

These specimens are badly damaged or otherwise unidentifiable and probably represent several species.

PARALEPIDIDAE

106. *Sudis atrox* Rofen.

Figures 24 and 25A.

80.160, C6208, (1) 21.5 mm.

The genus *Sudis* of the monotypic subfamily Sudinae was for many years known only from the eastern Atlantic off Madeira and the Mediterranean as *Sudis hyalina* Rafinesque. The larval stages of this species were described and illustrated by Sanzo (1918). A review of the genus *Sudis* was presented by Harry (1951 :33–35). A new species from the eastern Pacific, *Sudis atrox*, was recently described by Rofen (1963: 5, fig.1). *S. atrox* was based on a 75-mm. SL holotype and "35 identifiable remains" taken from stomach contents of *Alepisaurus* and *Parethunnus sibi* at two stations several hundred kilometers west of Baja California. Fourteen specimens of *S. atrox*, 3.4 mm. Notochord Length to 12.5 mm. SL had been sorted from 13 stations of Norpac Expedition between Hawaii and the American mainland (E.H. Ahlstrom, personal communication).

FIGURE 24.—*Sudis atrox*. 21.5 mm. SL station 80.160, C6208.

107. *Lestidium ringens* (Jordan and Gilbert).

Figure 25A.

60.80, C6208, (1) 60 mm.; 60.120, B6203, (1) 72 mm.; 70.80, B6203, (1) 39 mm.; 80.80, H6204, (1) 53 mm.; 80.90, H6204, (2) 20–71 mm.; 80.100, H6204, (1) 78 mm.; 90.90, C6203, (35) 42–64 mm.; 90.120, H6204, (1) 28 mm.; 100.40, H6204, (1) 150 mm.

The 35 specimens taken in the *Cobb* pelagic trawl at station 90.90 indicate that this species may occur in large schools at least in certain areas. It has been identified from a large number of routine CalCOFI plankton-tow stations, but only one or a few specimens had been taken in a single tow. *Lestidium elongatum* Ege is undoubtedly a junior synonym of this species (E. H. Ahlstrom and R. R. Rofen, personal communications). The specimen reported as *Macroparalepis* sp. by Harry (1953:186, fig. 5) is a young stage of *L. ringens*.

108. *Notolepis rissoi* (Bonaparte).

Figure 25A.

70.200, H6204, (1) 59 mm.; 80.160, C6208, (2) ca. 37–ca. 65 mm.; 80.200, C6208, (1) ca. 30 mm.; 90.120, C6208, (10) 32–49 mm.

This species has generally been designated under the name of *Notolepis coruscans* (Jordan and Gilbert) (R. R. Rofen, personal communication). Our relatively small and mostly damaged specimens have lower numbers of anal fin rays (a maximum of 26 or 27) than other eastern Pacific specimens that have been reported (A. 29 to 33) (Harry, 1953:210).

109. *Macroparalepis macrurus* Ege.

Figure 25A.

70.200, H6204, (1) 41.5 mm.; 80.160, C6208, (1) ca. 59 mm.; 80.170, C6208, (1) ca. 73 mm.; 80.180, H6204, (1) 135 mm.; 80.200, C6208, (4) ca. 42–ca. 74 mm.; 90.80, C6208, (1) ca. 70 mm.; 90.100, C6208, (1) ca. 62 mm.; 90.120, C6208, (13) 67–77 mm.; 90.140, C6208, (1) ca. 72 mm.; 90.150, C6208, (73) ca. 61–82 mm.; 90.200, H6204, (1) ca. 27 mm.

This species is more widespread in the eastern Pacific, and perhaps more gregarious, than previously shown. The larvae have been taken in offshore plankton-net collections, but most catches had only one or two individuals. Most of the records reported by Ege (1957:94–95) are of single specimens; the maximum at one station was nine. The 73 specimens taken at station 90.150 in September by the *Cobb* pelagic trawl indicate that the species is at times locally abundant.

The above records extend the known range of the species. Previously Ege (1957:68) had recorded it from northeast of the Galapagos Islands. Harry (1953:231) placed this species in the genus *Stemnosudis* Harry, but our specimens, and apparently those of Ege, possess characters more like those of *Macroparalepis*. The 135-mm. specimen, one of the largest specimens of the species to be recorded, has the anterior lateral line scales only slightly higher than long (1.17X), the nostrils well in advance of a vertical line through the posterior end of the maxillary, D. 8, A. 38, vertebrae 96 total and 33 prehaemal, and the anterior peritoneal pigment spots coalesced (about 14 were present).

SCOPELARCHIDAE

110. *Benthalbella dentata* (Chapman).

Figure 25B.

83.90, C6303, (1) 43.5 mm.; 83.77, C6303, (1) 42 mm.; 87.80, C6303, (1) 118 mm.; 100.65, C6303, (1) 200 mm.; 108.63, C6303, (1) 167 mm.

Chapman (1939:530) described this species in the new genus he proposed, *Neoscopelarchoides*. Marshall (1955:314) used this generic name rather than *Benthalbella* Zugmayer 1911. These two generic names, however, are synonymous, and under the current International Rules of Zoological Nomenclature, *Benthalbella* has priority (E. H. Ahlstrom, personal communication).

FIGURE 25.—Locations of capture of: A, *Sudis atrox*, *Lestidium ringens*, *Notolepis rissoi*, *Macroparalepis macrurus*. B, *Benthalbella dentata*, *Scopelarchus nicholsi*, *Scopelarchus guentheri*, *Scopelarchus* sp., *Evermannella indica*. C, *Anotopterus pharao*, *Bathyleptus lisae*, *Ditropichthys* sp., *Cololabis saira*. D, *Serrivomer sector*, *Nemichthys scolopaceus*.

111. *Scopelarchus nicholsi* (Parr).

Figure 25B.

120.50, H6204, (1) 42.5 mm.; 120.80, H6204, (1) 62 mm.

112. *Scopelarchus guentheri* Alcock.

Figure 25B.

108.63, C6303, (1) 50 mm.; 110.35, C6303, (1) 46 mm.

113. *Scopelarchus* sp.

Figure 25B.

84.70, C6303, (1) 28 mm.; 90.47, C6208, (1) 26 mm.; 97.40, C6303, (2) 37 mm.; 110.46, C6303, (1) 28 mm.

There is a very good possibility that these specimens represent an undescribed species.

EVERMANNELLIDAE

114. *Evermannella indica* Brauer.

Figure 25B.

120.90, H6204, (1) 55.5 mm.

ANOTOPTERIDAE

115. *Anotopterus pharao* Zugmayer.

Figure 25C.

60.180, H6204, (1) 173 mm.; 90.120, H6204, (1) 80.5 mm.; 90.160, H6204, (1) 59 mm.; 100.140, H6204, (1) ca. 179 mm.; 100.160, H6204, (2) 96–103 mm.

APODES

DERICHTHYIDAE

116. *Derichthys serpentinus* Gill.

Figure 26A.

108.63, C6303, (1) 200 mm.

This specimen and one in the collections of Scripps Institution of Oceanography from about 215 km. (135 miles) southward of Punta Eugenia are the first records of this species from this area.

CYEMIDAE

117. *Cyema atrum* Günther.

Figure 26A.

60.70, H6204, (1) 101+ mm.; 60.100, H6204, (1) 145+ mm.; 60.140, H6204, (1) 126+ mm.; 60.180, H6204, (1) 131+ mm.; 70.200, H6204, (1) 106+ mm.; 80.100, H6204, (1) 96+ mm.; 83.90, C6203, (1) 50 mm.; 90.120, H6204, (1) 107+ mm.; 100.60, H6204, (1) 115+ mm.; 100.80, H6204, (1) 100+ mm.; 100.160, H6204, (3) 125–134+ mm.; 110.160, H6204, (1) 147+ mm.; 120.50, H6204, (1) 110+ mm.

SERRIVOMERIDAE

118. *Serrivomer sector* Garman.

Figure 25D.

60.60, H6204, (1) 557+ mm.; 83.77, C6303, (1) 582 mm.; 84.70, C6303, (1) 461 mm.; 86.92, C6303, (15) 312–645 mm.; 87.80, C6303, (4) 500–541 mm.; 87.90, C6303, (2) 436–537 mm.; 100.60, H6204, (1) 461+ mm.; 100.65, C6303, (1) 386 mm.; 108.63, C6303, (2) 532–574 mm.; 110.120, H6204, (1) 490+ mm.; 120.70, H6204, (1) 532+ mm.

NEMICHTHYIDAE

119. *Avocettina bowersi* (Garman).

Figure 26A.

60.100, H6204, (1) 551 mm.; 84.67, C6303, (1) 320 mm.; 86.92, C6303, (8) 395–675 mm.; 87.80, C6303, (5) 319–550 mm.; 87.90, C6303, (2) 460–462 mm.; 90.110, C6303, (1) 229 mm.; 90.160, H6204, (1) 445+ mm.; 93.100, C6303, (2) 395–485 mm.; 100.100, H6204, (1) 612 mm.; 110.120, H6204, (1) 541 mm.; 120.70, H6204, (1) 532 mm.; 120.80, H6204, (1) 499+ mm.; 123.50, B6203, (5) ca. 364–510 mm.

120. *Nemichthys scolopaceus* Richardson.

Figure 25D.

60.140, H6204, (1) 453 mm.; 60.160, B6203, (1) 477 mm.; 60.200, H6204, (1) 621 mm.; 70.80b, B6203, (1) 545+ mm.; 70.80, C6208, (1) 500+ mm.; 73.200, B6203, (1) 392 mm.; 80.90, H6204, (1) 561 mm.; 80.160, C6208, (5) 108–252 mm,; 90.70, H6204, (1) 273 mm.; 90.140, H6204, (1) 442 mm.; 90.160, C6208, (17) 118–220 mm.; 97.40, C6303, (2) 300–350 mm.; 100.40, C6303, (1) 406 mm.; 100.65, C6303, (1) 525 mm.; 120.45, H6204, (1) 761 mm.; 120.60, H6204, (1) 607 mm.; 123.50, B6203, (1) 761 mm.

121. Nemichthyidae, unidentified.

120.70, H6204, (1) 327+ mm.

This specimen is badly damaged.

CONGRIDAE

122. *Ariosoma gilberti* (Ogilby).

Figure 26A.

137.35, B6212, (3) 135–223 mm.; 140.35, B6212, (1) 145 mm.; 147.30, B6212, (1) 155 mm.

123. Congridae, unidentified.

133.35, B6212, (1) 144 mm.

This *Congrina* "like" specimen is damaged.

OPHICHTHYIDAE

124. Ophichthyidae, unidentified.

137.35, B6212, (1) 71 mm.; 143.30, B6212, (1) 121 mm.

These leptocephali have not been otherwise identified.

SYNENTOGNATHI

SCOMBERESOCIDAE

125. *Cololabis saira* (Brevoort).

Figure 25C.

60.200, B6203, (1) 66 mm.; 70.200, H6204, (1) 57 mm.; 80.100, B6203, (1) 69 mm.; 84.92, B6303, (1) 31.5 mm.; 127.45, B6212, (1) 25 mm.

ANACANTHINI

MORIDAE

126. *Melanonus zugmayeri* Norman?

Figure 26B.

60.90, H6204, (1) 112 mm.; 60.160, H6204, (1) 120 mm.; 86.92, C6303, (1) 214 mm.; 87.80, C6303, (1) 115 mm.; 108.63, C6303, (2) 148–209 mm.

These specimens are tentatively identified as this species pending further study (D. M. Cohen, personal communication).

GADIDAE

127. *Merluccius products* (Ayres).

Figure 26B.

60.55, C6208, (7) 179–414 mm.; 65.54, C6208, (1) 265 mm.; 70.51, C6208, (186) 150–244 mm.; 80.55, H6204, (1) 166 mm.; 80.60, C6208, (4) 375–415 mm.; 80.70, H6204, (1) 10.5 mm.; 80.80, H6204, (2) 9–10 mm.; 80.90, H6204, (9) 7.5–10 mm.; 80.100, H6204, (12) 6–11 mm.; 82.45, C6208, (38) 80–220 mm.; 82.69, C6303, (38) 285–518 mm.; 83.70a, B6303, (1) 471 mm.; 83.70, C6303, (9) 327–505 mm.; 83.77, C6303, (5) 299–361 mm.; 84.67, C6303, (4) 396–504 mm.; 84.70, C6303, (2) 374–478 mm.; 84.71, C6303, (1) 492 mm.; 90.45a, H6105, (1) juvenile, damaged; 90.47, C6208, (3) 192–345 mm.; 90.48a, H6105, (3) 16–25.5 mm.; 90.48b, H6105, (33) 17–31.5 mm.; 90.48c, H6105, (6) 20.5–36 mm.; 94.28b, C6208, (1) 430 mm.; 94.30, C6208, (7) 162–420 mm.; 94.32b, B6204, (1) 17 mm.; 95.31d, B6204, (3) 19.5–36.5 mm.; 97.40, C6303, (29) 327–688 mm.; 99.31, C6208, (2) 192–370 mm.; 100.40, H6204, (4) 20–22 mm.; 100.40, C6203, (1) 398 mm.; 110.35, H6204, (1) 23 mm.; 110.35, C6303, (131) 244–577 mm.; 110.36, C6303, (3) 376–496 mm.; 111.36a, C6303, (495) ca. 258–598 mm.; 111.36b, C6303, (ca. 300) ca. 239–515 mm.; 111.37a, C6303, (65) 282–479 mm.; 113.34a, C6303, (8) 20.5–392 mm.; 120.45, H6204, (2) 19–23 mm.; 120.45, B6212, (1) 266 mm.; 120.50, H6204, (2) 31–34.5 mm.; 120.60, H6204, (1) 23.5 mm.; 147.30, B6212, (8) 105–150 mm.

MACROURIDAE

128. *Coryphaenoides acrolepis* (Bean)?

Figure 26B.

60.60, H6204, (1) 515 mm.

The species of this genus in this area are confused, and this identification must be tentative until the problems are resolved.

129. Macrouridae, unidentified.

86.92, C6303, (2) 333–347 mm.

These two specimens from about 305 km. (190 miles) SW. of Point Conception, Calif., represent an undescribed genus and species of bathypelagic macrouroid (C. L. Hubbs, personal communication).

130. Macrouridae, unidentified.

100.40, H6204, (1) 32 mm.

This specimen is too small to identify without comparative material.

LOPHOBRANCHII

SYNGNATHIDAE

131. *Syngnathus arcta* (Jenkins and Evermann).

90.45, H6105, (1) 166 mm.; 95.31b, B6204, (1) 72 mm.

ALLOTRIOGNATHI

TRACHIPTERIDAE

132. *Desmodema polystictum* (Ogilby).

Figure 26C.

89.90, C6303, (1) 614 mm.; 90.160, C6208, (1) 1,106 mm.; 100.80, H6204, (1) 455+ mm.

133. *Trachipterus t. altivelis* Kner.

Figure 26C.

60.90, C6208, (2) 49.5–1,435 mm.; 70.60, C6208, (1) 1,014 mm.; 80.52, C6208, (2) 177–297 mm.; 82.45, C6208, (2) 187–275 mm.; 85.68, C6303, (1) 133 mm.; 86.92, C6303, (1) 605 mm.; 90.47, C6208, (1) 1,000 mm.; 93.29, C6208, (1) 445 mm.

LOPHOTIDAE

134. *Lophotus* sp.

Figure 26C.

80.170, C6208, (1) 46.5 mm.

This specimen is too small to allow specific identification (J. E. Fitch, personal communication).

BERYCOMORPHI

MELAMPHAIDAE

135. *Scopelogadus mizolepis bispinosus* (Gilbert).

Figure 26D.

60.60, H6204, (2) 24–72 mm.; 60.80, C6208, (1) 33 mm.; 60.90, H6204, (3) 18–51 mm.; 60.100, H6204, (2) 13–75

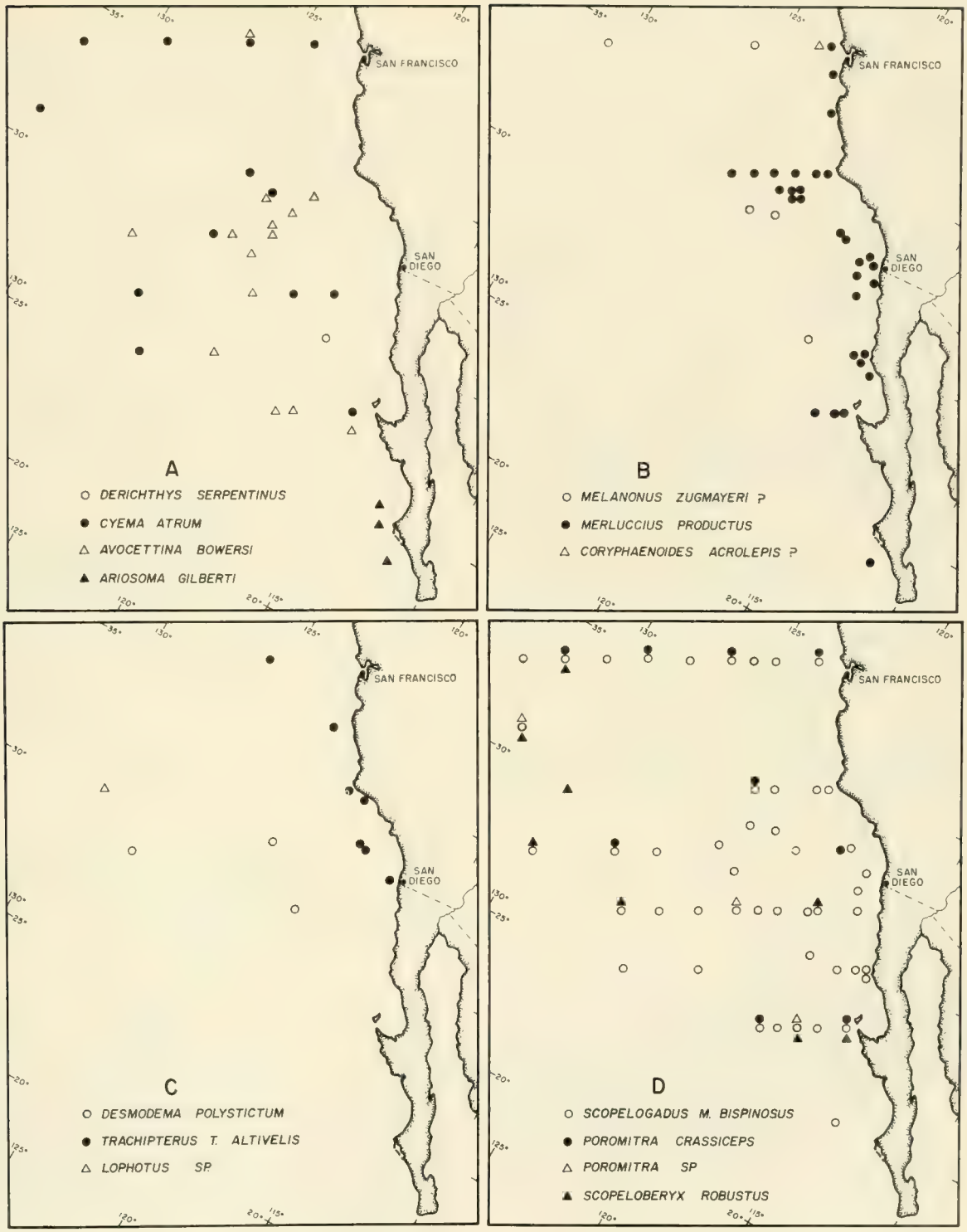

FIGURE 26.—Locations of capture of: A, *Derichthys serpentinus, Cyema atrum, Avocettina bowersi, Ariosoma gilberti.* B, *Melanonus zugmayeri?, Merluccius productus, Coryphaenoides acrolepsis?,* C, *Desmodema polystictum, Trachipterus trachipterus altivelis, Lophotus* sp. D, *Scopelogadus mizolepis bispinosus, Poromitra crassiceps, Poromitra* sp., *Scopeloberyx robustus.*

mm.; 60.120, H6204, (10) 63–75 mm.; 60.140, H6204, (1) 67 mm.; 60.160, H6204, (2) 64–75 mm.; 60.180, H6204, (2) 30–43 mm.; 60.200, B6203, (1) 53 mm.; 70.200, H6204, (1) 28 mm.; 80.55, H6204, (1) 63 mm.; 80.60, H6204, (2) 18–68 mm.; 80.80, H6204, (7) 45–60 mm.; 80.90, B6203, (2) 41–47 mm.; 80.90, H6204, (3) 65–79 mm.; 86.92, C6303, (13) 25–90 mm.; 87.90, C6303, (8) 29–90 mm.; 90.45a, H6105, (1) 47 mm.; 90.70, H6204, (11) 45–68 mm.; 90.70, C6208, (3) 61–70 mm.; 90.110, B6203, (1) 70 mm.; 90.140, H6204, (2) 66–74 mm.; 90.160, H6204, (2) 21–44 mm.; 90.160, C6208, (2) 56–58 mm.; 93.100, C6303, (1) 35 mm.; 94.32a, B6204, (2) 56–58 mm.; 97.40, C6303, (12) 36–45 mm.; 100.40, H6204, (2) 54–55 mm.; 100.40, C6303, (1) 49 mm.; 100.60, H6204, (5) 56–82 mm.; 100.65, C6303, (17) 43–76 mm.; 100.80, H6204, (4) 20–52 mm.; 100.90, H6204, (5) 34–74 mm.; 100.100, H6204, (3) 35–54 mm.; 100.120, H6204, (1) 56 mm.; 100.140, H6204, (1) 53 mm.; 100.160, H6204, (3) 25–64 mm.; 108.63, C6303, (26) 45–87 mm.; 110.35, H6204, (1) 62 mm.; 110.35, C6303, (2) 30–43 mm.; 110.40, H6204, (1) 45 mm.; 110.50, B6203, (2) 55.5 mm.; 110.120, H6204, (3) 18–79 mm.; 110.160, H6204, (5) 10–83 mm.; 120.45, H6204, (1) 54 mm.; 120.60, H6204, (1) 55 mm.; 120.70, H6204, (6) 45–62 mm.; 120.80, H6204, (3) 28–51 mm.; 120.90, H6204, (3) 46–83 mm.; 137.50, B6203, (5) 26–58 mm.

This species, previously known as *Melamphaes bispinosus* or *Scopelogadus bispinosus*, has recently been shown to be a subspecies of *Scopelogadus mizolepis* (Günther) by Ebeling (1963:19).

136. *Poromitra crassiceps* (Günther).

Figure 26D.

60.60, H6204, (1) 127 mm.; 60.100, H6204, (1) 117 mm.; 60.140, H6204, (1) 30 mm.; 60.180, H6204, (2) 22–45.5 mm.; 80.90, H6204, (1) 24 mm.; 90.48b, H6105, (1) 25 mm.; 90.160, C6208, (2) 91–96 mm.; 120.45, H6204, (1) 89 mm.; 120.90, H6204, (2) 92–97 mm.

This species has been listed under the name of its junior synonym, *Poromitra cristiceps* (Gilbert).

137. *Poromitra* sp.

Figure 26D.

70.200, H6204, (2) 51–64 mm.; 100.100, H6204, (1) 70 mm.; 120.70, H6204, (1) 75 mm.

These specimens, with relatively small eyes and a low number of dorsal fin rays (III, 10 or 11) are representative of a new species. This was called to our attention by A. W. Ebeling (personal communication), who is preparing a detailed description for publication.

138. *Scopeloberyx robutus* (Günther).

Figure 26D.

60.180, H6204, (1) 31 mm.; 70.200, H6204, (2) 18–21 mm.; 80.180, C6208, (1) 12 mm.; 90.200, H6204, (2) 31.5–32 mm.; 100.60, H6204, (1) 71.5 mm.; 100.160, H6204, (6) 18–32 mm.; 120.45, H6204, (3) 57–59 mm.; 120.70, H6204, (1) 60 mm.

This species has generally been known in this area as *Scopeloberyx nycterinus* (Gilbert). The synonymy of *S. nycterinus* with *S. robustus* has recently been determined by A. W. Ebeling (personal communication).

139. *Melamphaes acanthomus* Ebeling.

Figure 27A.

90.45a, H6105, (2) 83–92 mm.; 100.65, C6303, (1) 81 mm.

140. *Melamphaes indicus* Ebeling.

Figure 27A.

90.160, H6204, (1) 35.5 mm.

This record extends the known range of this species eastward from west of the Hawaiian Islands, as delimited by Ebeling (1962, fig. 47).

141. *Melamphaes laeviceps* Ebeling.

Figure 27B.

60.200a, B6203, (2) 28–29 mm.; 60.200, H6204, (1) 27 mm.; 73.200, B6203, (4) 24–29 mm.; 80.200, C6208, (3) 27–28 mm.; 87.200, B6203, (1) 27 mm.; 90.150, C6208, (1) 26 mm.; 90.160, H6204, (1) 28 mm.; 100.140, H6204, (1) 28 mm.

This species previously has only been reported from the tropical eastern and central Pacific (Ebeling, 1962, fig. 53).

142. *Melamphaes longivelis* Parr.

Figure 27B.

90.120, H6204, (1) 33 mm.

This specimen represents a range extension for the species of about 260 km. (160 miles) northeast from that shown by Ebeling (1962:77, not fig. 44).

143. *Melamphaes lugubris* Gilbert.

Figure 27B.

60.60, H6204, (2) 30–84 mm.; 60.80, H6204, (1) 55 mm.; 60.80, C6208, (1) 19 mm.; 60.90, H6204, (3) 22–79 mm.; 60.120, B6203, (2) 38 mm.; 70.80b, B6203, (1) 37 mm.; 80.55, H6204, (3) 38–41 mm.; 80.60, H6204, (1) 44 mm.; 80.75, B6303, (1) 17 mm.; 80.80, H6204, (3) all ca. 40 mm.; 80.90, H6204, (5) 37–43 mm.; 80.100, B6203, (1) 37 mm.; 80.100, H6204, (2) 20–22 mm.; 80.110, B6203, (1) 13 mm.; 83.77, C6303, (1) 22 mm.; 84.92, B6303, (7) 36–39 mm.; 86.92, C6303, (5) 36–52 mm.; 87.80, C6303, (4) 35–38 mm.; 90.45a, H6105, (4) 51–77 mm.; 90.70, H6204, (2) 40–43 mm.; 90.70, C6208, (7) 25.5–50 mm.; 97.40, C6303, (7) 31–36 mm.; 97.50, B6203, (1) 38 mm.; 100.60, H6204, (1) 21 mm.; 100.65, C6303, (1) 38 mm.; 108.63, C6303, (2) 32–37 mm.

144. *Melamphaes macrocephalus* Parr.

Figure 27A.

120.90, H6204, (1) 116 mm.

145. *Melamphaes parvus* Ebeling.

Figure 27A.

60.120, B6203, (1) 25.5 mm.; 60.120, H6204, (2) 35–37.5 mm.; 60.140, H6204, (4) 36–45 mm.; 60.160, B6203, (3) 36–48 mm.; 60.180, H6204, (1) 27 mm.; 80.80, H6204, (3) 37–38 mm.; 80.90, B6203, (1) 36 mm.; 80.90, H6204, (1) 45 mm.; 80.200, C6208, (1) 18 mm.; 82.69, C6303, (2) 33–38 mm.; 84.92, B6303, (3) 43–47 mm.; 86.92, C6303, (5) 33–44 mm.; 87.80, C6303, (2) 38–43 mm.; 90.70, H6204, (2) ca. 38 mm.; 97.40, C6303, (1) 39 mm.; 100.60, H6204, (1) 41 mm.; 100.65, C6303, (20) 31–48 mm.; 100.160, H6204, (1) 18 mm.; 108.63, C6303, (6) 30–43 mm.

146. *Melamphaes suborbitalis* (Gill).

Figure 27B.

60.180, H6204, (1) 37 mm.

147. *Melamphaes* spp.

60.200, H6204, (1) 15 mm.; 80.80, H6204, (1) 17 mm.; 133.35, B6212, (1) 15 mm.

These damaged specimens probably represent more than one species.

ANOPLOGASTERIDAE

148. *Anoplogaster cornuta* (Valenciennes).

Figure 27A.

80.200, C6208, (1) 94 mm.; 86.92, C6303, (7) 86–121 mm.; 87.80, C6303, (1) 94.5 mm.; 90.45a, H6105, (1) 94 mm.; 108.63, C6303, (1) 88 mm.

As pointed out by Grey (1955:293), *Caulolepis longidens* Gill is a junior synonym of this species.

PERCOMORPHI

CARISTIIDAE

149. *Caristius macropus* (Bellotti).

Figure 29A.

83.77, C6303, (1) 165 mm.

150. *Caristius maderenis* Maul?

Figures 28 and 29A.

108.63, C6303, (2) 148–160 mm.

The phylogenetic position of the Caristiidae and the true identity of these specimens are under study (C. L. Hubbs, personal communication).

SERRANIDAE

151. Serranidae, unidentified.

140.30, B6212, (6) 9–12 mm.

These specimens are too small to identify without comparative material.

CHEILODIPTERIDAE

152. *Howella brodiei* (Ogilby)?

Figure 29A.

60.120, B6203, (2) 52.5–70.5 mm.; 60.160, H6204, (1) 71 mm.; 80.80, H6204, (1) 29.5 mm.; 80.90, H6204, (3) 30.5–34 mm.; 100.80, H6204, (1) 36 mm.

The generic limits and the intrageneric components of *Howella* Ogilby 1898 are not definitive at this time. It apparently contains as synonyms the genera *Galeagra* Heller and Snodgrass 1903 and *Rhectogramma* Norman 1930; and, also apparently, these genera should be included in the family Cheilodipteridae (rather than Serranidae). The above specimens may represent a new species, but their characters are close to the descriptions given by Ogilby (1898:734) for *H. brodiei* from Lord Howe Island, and are similar to the accounts of this species from the Philippines given by Herre and Herald (1951:330) and from the North Atlantic Ocean by Koefoed (1952:5). Other specimens of *Howella* from the equatorial eastern Pacific that we have examined are specifically distinct from these tentatively designated as *H. brodiei*, and appear to be the *Galeagra pammelas* of Heller and Snodgrass. The monotypic *Sphyraenops bairdianus* Poey that has at times been placed in this complex apparently is generically distinct.

CARANGIDAE

153. *Trachurus symmetricus* (Ayres).

Figure 29A.

68.50, C6208, (1) 180 mm.; 70.80, C6208, (25) 64.5–503 mm.; 70.90, C6208, (1) 61 mm.; 70.100, C6208, (1) 60 mm.; 80.70, C6208, (1) 65 mm.; 80.80, C6208, (9) 28–69 mm.; 90.48b, H6105, (1) ca. 5 mm.; 90.49b, C6208, (12) 51–224 mm.; 90.80, C6208, (5) 23.5–64.5 mm.; 90.150, C6208, (1) 40 mm.; 91.39a, C6208, (1) 190 mm.; 91.39b, C6208, (3) 100–240 mm.; 93.26, C6208, (2) 100–125 mm.; 94.28b, C6208, (1) 435 mm.; 94.29b, C6208, (3) 335 mm.; 94.29c, C6208, (12) ca. 125 mm.; 99.31, C6208, size and number not recorded, discarded at sea; 113.34a, C6303, (1) 63 mm.; 120.50, H6204, (1) 23 mm.

Nine of the above records of jack mackerel were based on larvae or small juveniles. One of these was taken about 420 miles offshore (90.150, C6208). At station 70.80, C6208, about 185 km. (115 miles) offshore, a night surface drag with the *Cobb* trawl caught 1 small juvenile and 24 spawning and spent males and females.

FIGURE 27.—Locations of capture of: A, *Melamphaes acanthomus, Melamphaes indicus, Melamphaes macrocephalus, Melamphaes parvus, Anoplogaster cornuta.* B, *Melamphaes laeviceps, Melamphaes longivelis, Melamphaes lugubris, Melamphaes suborbitalis.* C, *Citharichthys sordidus, Citharichthys xanthostigma, Citharichthys stigmaeus, Bothus leopardinus.* D, *Microstomus pacificus, Glyptocephalus zachirus, Eopsetta jordani.*

CORYPHAENIDAE

154. *Coryphaena hippurus* Linnaeus.

147.30, B6212, (1) ca. 24 mm. damaged.

This specimen was taken about 80 km. (50 miles) offshore, south of Almejas Bay, Baja California.

STROMATEIDAE

155. *Cubiceps gracilis* (Lowe).

Figure 29B.

80.180, C6208, (2) 32.5–47 mm.; 80.190, C6208, (2) 31–40.5 mm.

Two recognized species of *Cubiceps* occur in the eastern Pacific, and *C. gracilis* appears to be the most suitable name to apply to the above specimens. The other species, *C. carinatus* Nichols and Murphy (1944: 245), has fewer dorsal and anal fin softrays, fewer lateral line scales, and a more tropical distribution.

156. *Icichthys lockingtoni* Jordan and Gilbert.

Figure 29B.

60.80, H6204, (3) 11–15 mm.; 60.140, H6204, (2) 98–193 mm.; 70.80, B6203, (6) 20.5–27 mm.; 80.60, H6204, (1) 19 mm.; 80.90, B6203, (4) 20–46 mm.; 80.90, H6204, (13) 11–44.5 mm.; 80.100, B6203, (1) 19.5 mm.; 80.100, H6204, (2) 9–10.5 mm.; 80.120, B6203, (1) 14.5 mm.; 83.70a, B6303, (5) 27–42.5 mm.; 83.70c, B6303, (1) 32.5 mm.; 83.77, C6303, (1) 29.5 mm.; 90.45b, H6105, (1) 26 mm.; 90.48c, H6105, (1) 57.5 mm.; 90.80, C6208, (1) 40 mm.; 90.120, H6204, (1) 8 mm.; 94.29d, C6208, (3) 81–95 mm.; 100.65, C6303, (1) 39 mm.

157. *Palometa simillima* (Ayres).

Figure 29B.

80.52, C6208, (3) 51.5–61 mm.; 82.45, C6208, (1) 48 mm.; 93.26, C6208, (83) ca. 50–75 mm.; 94.28a, C6208, (2) small, size not recorded, discarded at sea; 94.28b, C6208, (4) ca. 50–75 mm.; 94.29b, C6208, (37) 78–147 mm.; 94.29c, C6208, (3) ca. 50 mm.; 99.31, C6208, (32) 85–165 mm.; 120.50, H6204, (7) 12–20 mm.

TETRAGONURIDAE

158. *Tetragonurus cuvieri* Risso.

Figure 29B.

100.65, C6303, (1) 51 mm.; 88.105a, B6303, (1) 37 mm.

When first seen in the cod end of the collapsible net, the 37-mm. specimen was alive within the cavity of a pyrosome. A few records of association of *T. atlanticus* Lowe and *T. cuvieri* with medusae were summarized by Mansueti (1963: 59–60).

BRAMIDAE

159. *Brama japonica* Hilegendorf.

Figure 29C.

70.80, C6208, (3) 215–220 mm.; 70.200, H6204, (1) 15.5 mm.; 80.180, C6208, (1) 52.5 mm.

Two names previously used for pomfrets from the North Pacific, *B. brama* (Bonnaterre) and *B. raii* (Bloch), do not apply to this species (G. W. Mead, personal communication).

160. *Pteraclis velifera* (Pallas)?

Figure 29C.

110.160, H6204, (1) 9.5 mm.

This small specimen can be identified only tentatively at this time (G. W. Mead, personal communication).

GEMPYLIDAE

161. *Gempylus serpens* Cuvier.

Figure 29C.

70.200, H6204, (1) 28 mm.; 80.180, C6208, (1) 52 mm.; 90.180, C6208, (1) 105 mm.

TRICHIURIDAE

162. *Lepidopus xantusi* Goode and Bean.

Figure 29C.

113.34a, C6303, (2) 230–249 mm.

SCOMBRIDAE

163. *Sarda lineolata* (Girard).

92.28, C6208, (3) 2–3 kg., discarded at sea, no length record taken; 93.26, C6208, (8) 2–4 kg., no length record; 93.28, C6208, (60) 340–490 mm.; 94.28b, C6208, (18) all ca. 300 mm.; 94.29b, C6208 (1) 335 mm.; 94.29c, C6208, (1) 4 kg., no length record; 94.30, C6208, (20) 2–4 kg., no length record; 95.30, C6208, (11) 2–4 kg., no length record; 113.34b, C6303, (1) adult, no size record.

These records are of adult fish taken close inshore and generally near the surface.

164. *Scomber japonicus* Houttuyn.

90.49b, C6208, (1) 288 mm.; 99.31, C6208, (16) 300–340 mm.

This species has also been referred to as *Scomber diego* Ayres, *Pneumatophorus japonicus*, and *Pneumatophorus diego*. This complex apparently also includes *Scomber colias* Gmelin of the Atlantic, and has previously been cited as such by various authors (B. B. Collette, personal communication).

FIGURE 28.—*Caristius maderensis?*, 160 mm. SL, station 108.63, C6303.

SCIAENIDAE

165. *Seriphus politus* Ayres.

93.25, C6208, (1) 175 mm.; 94.29c, C6208, (3) 165–186 mm.

166. *Roncador stearnsi* (Steindachner).

93.26, C6208, (131) ca. 150–175 mm.

SPHYRAENIDAE

167. *Sphyraena argentea* Girard.

93.26, C6208, (4) 260–325 mm.

CHIASMODONTIDAE

168. *Chiasmodon niger* Johnson.

120.90, H6204, (1) 47.5 mm.

This specimen was taken about 320 km. (200 miles) west of Punta Eugenia, Baja California.

169. *Kali* sp.

100.100, H6204, (1) 172 mm.

This specimen was taken about 480 km. (300 miles) west of Rosario Bay, Baja California. It cannot be specifically identified from current references, and the generic limits of *Kali* are confused two genera appear to be included under this one name (D. M. Cohen, personal communication). Compared to specimens identified as *K. indica* (Lloyd) and *K. normani* (Parr) in the collections of Scripps Institution of Oceanography, this specimen is unique in having a reduced number of broad-based, short, blunt teeth in both jaws.

170. *Pseudoscopelus scriptus* Lütken.

137.50, B6203, (1) 83.5 mm.

This specimen was taken about 160 km. (100 miles) west of Santa Maria Bay, Baja California. Parr (1933 : 36–42) considered *P. scriptus* to consist of two subspecies and also described a new species, *P. altipinnis*. The above specimen is closer to the description Parr gave for *P. scriptus*, but it is possible that the two species are synonymous (R. J. Lavenberg, personal communication).

SCORPAENIDAE

171. *Sebastolobus alascanus* Bean.

Figure 29D.

60.60, H6204, (1) 26 mm.

172. *Sebastolobus altivelis* Gilbert.

Figure 29D.

60.120, H6204, (1) 40.5 mm.; 80.55, H6204, (5) 30.5–39.5 mm.; 80.60, B6203, (1) 31 mm.; 80.60, H6204, (1) 29.5 mm.; 80.70, C6208, (1) 14.5 mm.; 80.80, H6204, (2) 33 mm.; 80.90, H6204, (1) 36 mm.; 84.92, B6303, (2)

FIGURE 29.—Locations of capture of: A, *Caristius macropus, Caristius maderensis?, Howella brodiei?, Trachurus symmetricus.* B, *Cubiceps gracilis, Icichthys lockingtoni, Palometa simillima, Tetragonurus cuvieri.* C, *Brama japonica, Pteraclis velifera?, Gempylus serpens, Lepidopus xantusi.* D, *Sebastolobus alascanus, Sebastolobus altivelis, Coryphopterus nicholsi.*

30–35 mm.; 90.32, H6204, (3) 34–47.5 mm.; 90.70, H6204, (1) 41.5 mm.; 90.70, C6208, (3) 13–15.5 mm.; 97.50, B6203, (3) 35.5–42 mm.; 100.40, H6204, (4) 39.5–45.5 mm.; 110.35, C6303, (4) 28–36.5 mm.

All these specimens are pelagic, prejuvenile specimens, taken from close inshore to 480 km. (300 miles) at sea.

173. *Sebastodes diploproa* (Gilbert).

91.39b, C6208, (100+) ca. 31–41 mm.

174. *Sebastodes saxicola* (Gilbert).

60.60, H6204, (5) 16–23 mm.

175. *Sebastodes proriger* (Jordan and Gilbert)?

60.60, H6204, (2) both 26.5 mm.

This identification is uncertain because of the small size of the specimens.

176. *Sebastodes goodei* Eigenmann and Eigenmann.

68.50, C6208, (8) 197–231 mm.

177. *Sebastodes jordani* (Gilbert).

94.30, C6208, (2) 188–192 mm.

178. *Sebastodes* spp.

60.60, H6204, (2) 10–13 mm.; 60.70, H6204, (1) •5.5 mm.; 70.80–5N, B6203, (1) 15 mm.; 80.90, B6203, (1) 15.5 mm.; 90.48a, H6105, (1) 4.5 mm.; 90.48b, H6105, (1) 21.5 mm.

Specific identifications were not made because of the small size of these specimens.

ANOPLOPOMATIDAE

179. *Anoplopoma fimbria* (Pallas).

68.50, C6208, (1) 182 mm.

ZANIOLEPIDAE

180. *Zaniolepis frenata* Eigenmann?

90.32, B6203, (1) 22 mm.; 113.34a, C6303, (1) 39.5 mm.

These two small specimens may represent the sympatric *Z. latipinnis* Girard—adequate comparable material is not available to confirm our identification. The larger specimen appears, however, to be *Z. frenata*, because its third anal spine is shorter than the second.

AGONIDAE

181. Agonidae, unidentified.

90.48a, H6105, (1) 20.5 mm.; 90.48b, H6105, (2) 24.5–24.5 mm.; 90.60, B6203, (1) 19 mm.; 113.34a, C6303, (1) 15.5 mm.

Comparative material is not available that will allow identification of these small specimens (J. E. Fitch, personal communication).

GOBIIDAE

182. *Coryphopterus nicholsi* (Bean).

Figure 29D.

60.140, H6204, (2) 20–29 mm.; 80.90, H6204, (1) 15.5 mm.

These specimens, taken about 560 and 260 km. (350 and 160 miles) offshore, appear to be pelagic, oceanic, protracted prejuvenile stages of this species, which is generally known as an inshore, shallow-water, benthic inhabitant. Other specimens of this form have been taken in offshore waters at various times in CalCOFI routine, 140-m.-deep plankton tows.

183. Gobiidae, unidentified.

90.48a, H6105, (2) 7–8 mm.

BATRACHOIDIDAE

184. *Porichthys notatus* Girard.

94.29c, C6208, (2) 98–133 mm.

185. *Porichthys* sp.

65.54, C6208, (1) 125 mm.

This specimen was not identified to species and was discarded at sea.

BLENNIIDAE

186. *Hypsoblennius gentilis* (Girard).

123.45, B6212, (1) 15 mm.

ZOARCIDAE

187. *Melanostigma pammelas* Gilbert.

90.45a, H6105, (1) 108 mm.

HETEROSTOMATA

BOTHIDAE

188. *Citharichthys sordidus* (Girard).

Figure 27C.

60.60, C6208, (1) 25 mm.; 70.51, C6208, (6) 27–36 mm.; 70.60, C6208, (1) 32 mm.; 70.80–5N, B6203, (1) 27 mm.; 80.60, B6203, (1) 25.5 mm.; 80.60, C6208, (3) 28–32 mm.; 84.92, B6303, (1) 16 mm.

These are all pelagic larval and juvenile specimens taken from close inshore to about 290 km. (180 miles) at sea.

189. *Citharichthys xanthostigma* Gilbert.

Figure 27C.

113.34a, C6303, (a) all ca. 22 mm.

190. *Citharichthys stigmaeus* Jordan and Gilbert.

Figure 27C.

60.60, H6204, (2) 32.5–38.5 mm.; 60.60, C6208, (1) 26.5 mm; 60.70, C6208, (1) 28.5 mm.; 60.80, C6208, (1) 32.5 mm.; 70.51, C6208, (6) 29.5–34 mm.; 80.60, C6208, (8) 24.5–30 mm.; 80.100, H6204, (2) 26.5–28 mm.; 83.70c, B6303, (1) 21 mm.; 83.90, C6303, (1) 22 mm.; 84.92, B6303, (1) 22 mm.; 90.45, H6105, (1) 29.5 mm.; 90.45a, H6105, (1) 29 mm.; 90.90, C6303, (14) 13–21.5 mm.; 90.48c, H6105, (2) 31 mm.; 97.40, C6303, (3) 23.5–26.5 mm.

These are all pelagic larval and juvenile specimens taken from close inshore to about 320 km. (200 miles) at sea.

191. *Citharichthys* sp.

67.50, C6208, (1) 150 mm.

This specimen was discarded at sea and not specifically identified.

192. *Bothus leopardinus* (Günther).

Figure 27C.

140.35, B6212, (2) 13–20 mm.

These specimens may be *B. constellatus* (Jordan), if *B. constellatus* is a distant species. Until distinction or synonymy can be established, we choose to use the earlier name.

PLEURONECTIDAE

193. *Microstomus pacificus* (Lockington).

Figure 27D.

70.51, C6208, (1) 28.5 mm.; 70.60, C6208, (1) 26.5 mm.; 80.70, H6204, (1) 21.5 mm.; 84.92, B6303, (1) 24 mm.; 97.40, C6303, (1) 30 mm.; 100.65, C6303, (2) 26–34 mm.; 100.160, H6204, (1) 42 mm.; 107.60, C6303, (1) 28.5 mm.

These larval specimens were taken from close inshore to about 840 km. (520 miles) off northern Baja California.

194. *Glyptocephalus zachirus* Lockington.

Figure 27D.

60.70, C6208, (1) 55.5 mm.; 60.90, C6208, (3) 36–62 mm.; 60.100, C6208, (1) 33 mm.; 70.60, C6208, (3) 39–45 mm.; 80.60, C6208, (1) 51 mm.

These larval specimens were taken about 55 to 315 km. (35 to 195 miles) offshore.

195. *Eopsetta jordani* (Lockington).

Figure 27D.

60.70, H6204, (1) 20 mm.

CYNOGLOSSIDAE

196. *Symphurus atricauda* (Jordan and Gilbert).

94.30, C6208, (1) 130 mm.

PLECTOGNATHI

MOLIDAE

197. *Mola mola* (Linnaeus).

94.28a, C6208, (13) "moderate size"; 94.28b, C6208, (4) 500–750 mm.; 94.29b, C6208, (3) all 380 mm.; 94.29c, C6208, 94.29d, C6208, (12) 378–1,460 mm.; (3) all ca. 450 mm.

PEDICULATI

ONEIRODIDAE

198. *Oneirodes eschrichtii* Lütken.

Figure 30.

80.80, H6204, (1) 52 mm.; 90.160, H6204, (1) 98 mm.; 100.140, H6204, (1) 25 mm.; 110.35, C6203, (1) 29 mm.; 120.45, H6204, (1) 26 mm.

These specimens fit the *O. eschrichtii* group as defined by Bertelsen (1951: 77–84), and further compare well with *O. eschrichtii s.s.* (R. H. Rosenblatt, personal communication).

199. *Oneirodes eschrichtii* Lütken?

Figure 30.

120.70, H6204, (2) 13.5–29.5 mm.

These two small specimens appear to represent this species (P. Struhsaker, personal communication).

200. *Oneirodes acanthias* (Gilbert)?

Figure 30.

123.50, B6203, (1) 24 mm.

This small specimen appears to represent this species (P. Struhsaker, personal communication).

201. *Chaenophryne parviconus* Regan and Trewavas.

Figure 30.

108.63, C6303, (1) 52 mm.

202. Oneirodidae, unidentified.

110.140, H6204, (1) 14 mm.

The identity of this free-living male is uncertain.

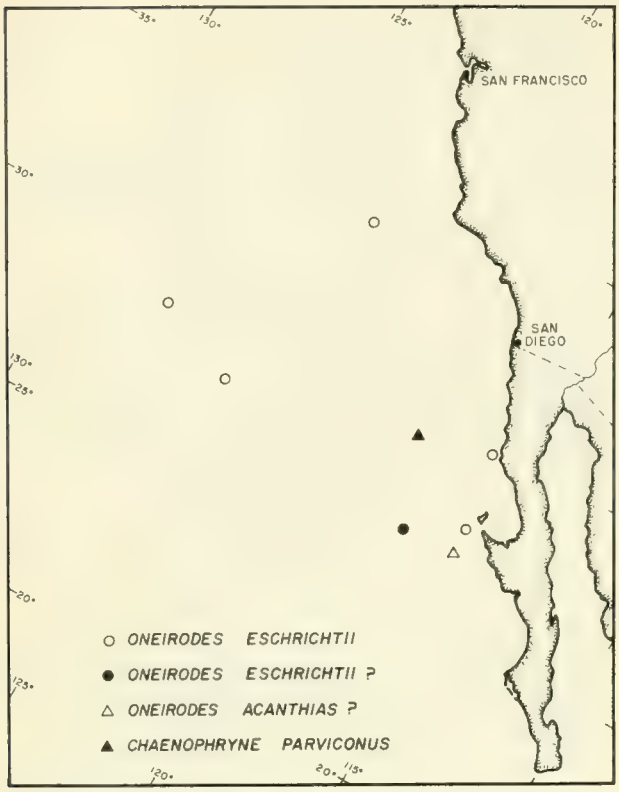

FIGURE 30.—Locations of capture of: *Oneirodes eschrichtii*, *Oneirodes eschrichtii?*, *Oneirodes acanthias?*, *Chaenophryne parviconus*.

ALPHABETICAL LIST OF FISHES

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COMPARISON OF TWO METHODS OF N-ETHYLCARBAZOLE CARBOHYDRATE ANALYSIS [1]

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Two currently used N-ethylcarbazole (NEC) methods for determining the amount of dissolved substances in sea water which respond to the NEC reagent and which will be referred to here as "carbohydrates," are the original one described by Erdman and Little [2] and the modification described by Zein-Eldin and May (1958). It has been assumed by many investigators that those methods give comparable results when used to estimate the amount of carbohydrates in water. Recently, however, data obtained through both methods at the Bureau of Commercial Fisheries Biological Laboratory in Galveston, Tex., suggested that their corresponding estimates differ significantly. This difference prompted us to determine experimentally if the two methods yield the same results when used to analyze the carbohydrate content of aliquots from the same sample.

The original method described by Erdman and Little consists of adding the NEC reagent (1 g./l. of 36 N H_2SO_4) to the sample in one step, warming the mixture in a water bath, and then comparing color density with that of similarly treated arabinose (D-(-)-Arabinose) standards. This procedure will be called the "one-step" method. The method described by Zein-Eldin and May is the same as the above except that the NEC reagent is added in two steps. We will therefore refer to this procedure as the "two-step" method. Results of both procedures are based on the density of color development when NEC reagent reacts with carbohydrates. Units are expressed in mg. equivalents of arabinose.

We compared the two methods by analyzing carbohydrate determinations obtained routinely from many samples with each procedure. The one-step method yielded significantly higher results (table 1).

TABLE 1.—*Concentration of carbohydrates in samples of water collected from Galveston Island's East Lagoon during the period February–August, 1963*

[Units are mg./l. of arabinose equivalents]

Date, 1963	Method		Date, 1963	Method	
	One-step	Two-step		One-step	Two-step
	Mg./l.	*Mg./l.*		*Mg./l.*	*Mg./l.*
Feb. 16	4.15	1.06	6–14	3.80	2.27
Feb. 19	4.00	.61	6–18	4.71	3.76
Mar. 1	3.80	1.98	6–21	3.92	2.32
Mar. 12	4.55	1.71	6–25	3.66	1.78
Mar. 15	4.35	2.61	6–28	4.64	3.25
Mar. 19	3.65	.78	7–2	5.69	3.90
Mar. 22	3.50	1.15	7–5	5.85	3.70
Mar. 26	3.20	.85	7–9	7.21	3.18
Mar. 29	2.55	.73	7–12	5.07	3.24
Apr. 2	3.11	1.86	7–16	4.28	3.03
Apr. 9	5.14	3.01	7–19	5.36	4.45
Apr. 23	3.17	2.33	7–23	4.28	2.58
May 8	4.06	1.98	7–26	6.50	3.48
May 10	3.43	2.15	7–30	4.71	3.15
May 14	3.91	2.36	8–2	5.07	2.94
May 17	3.94	2.02	8–7	5.07	2.18
May 21	3.28	2.13	8–9	7.85	3.03
May 24	2.31	2.24	8–13	4.57	2.67
May 28	3.03	1.71	8–16	5.00	3.51
May 31	3.60	2.25	8–20	4.07	2.70
June 4	4.13	2.70	8–21	2.55	2.47
June 7	3.33	1.99	8–22	3.60	2.36
June 11	4.58	2.63			

Upon investigating the reason for the differences noted between estimates secured by the two methods, we found that the color density resulting from interacting NEC and carbohydrates in natural waters varied only slightly with the method used. However, when the NEC reagent was added to standard or calibration samples that consisted of

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[2] Erdman, J. G. and A. B. Little, 1950. Analysis of marine coastal and estuarine waters, 50 pp. Multiple fellowship of Gulf Research and Development Co., Mellon Institute, Pittsburgh, Pa. (Unpublished.)

known concentrates of arabinose in distilled or saline water, the resulting color density varied with the method used. The variation was such

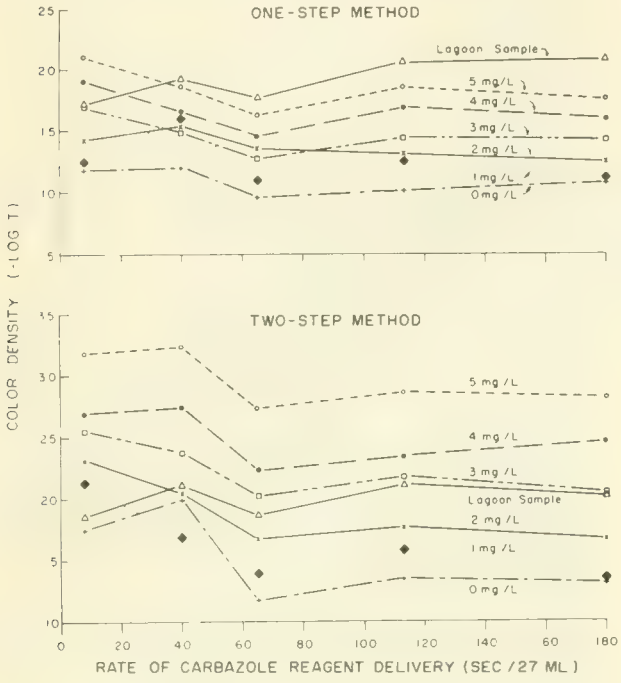

FIGURE 1.—Color density values obtained for six standard water samples and for one sample taken from Galveston Island's East Lagoon using two methods of carbohydrate analysis at five rates of reagent addition.

that estimates by the one-step method were higher than those obtained by the two-step method. We also found that the precision of estimates by either method is reduced if the reagent is added at a rate faster than about 27 ml.—the amount required by each procedure—per 65 seconds.

These conclusions become apparent from figure 1, which shows the raw data used to estimate the carbohydrate concentration in a water sample by both methods at various rates of reagent addition. If we consider only those portions of the curves from the 65-second addition rate and beyond, it can be seen that response of the carbohydrate in the sample to the NEC reagent corresponds to that of 6 to 7 mg./l. of arabinose by the one-step method, and 2.5 to 3 mg./l. by the two-step method. If the entire curves are considered, the sample estimates of carbohydrate concentration vary from about 0.3 to 7.0 mg./l. depending on the method used and also on the rate of reagent addition. The erratic results recorded when the reagent delivery rate was less than about 27 ml. per 65 seconds seem to be characteristic of both methods.

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RAPID METHOD FOR DETERMINING WATER CONTENT IN OYSTER TISSUE

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Medcof (1941) defined Condition Index (CI) as the ratio of the dry weight of the meat to the volume of the space between the valves × 1000. To dry the meat, Engle (1958) used 72 hours exposure at 90° C. in a convection-type oven. This will reduce a 25 g. sample to constant weight; however, it is frequently desirable to avoid the 72-hour waiting period.

Korringa (1956) reported a method by which the water content of oyster meats could be determined volumetrically using toluene distillation. The homogenized sample was placed in a flask and covered with toluene. The flask was connected to a condenser fitted with a distillation trap and maintained at 100° C. for 1 hour. The volume of water collected was measured and converted to weight. The total time required was about 1 hour. We were unable to get the reproducible accuracy desired because of the tenacity with which small droplets of water adhered to the sides of the condenser and fittings. To overcome this problem we devised a gravimetric adaptation of Korringa's method which eliminates the condenser and its associated problems and in which the weight of water is determined directly. This adaptation is discussed below.

Figure 1 shows all major components of the apparatus. The function of the intake drying tubes is to provide an atmosphere free of moisture. A 10 g. sample of homogenized oyster tissue is covered with toluene and heated to 100° C. for 45 minutes. The water vapor is collected in the tared outlet drying tubes. All tubes contain the drying agent, calcium chloride. Plastic check valves control direction of water vapor flow. The number of drying tubes needed can be determined by a trial run in which weights of the individual tubes are recorded. The last tube in direction of flow on both sides of the flask should not show a weight increase. In practice, once the proper number of tubes is determined, the tubes can be weighed as a unit. Suction should be applied very gently. With this method, we have been able to produce the same accuracy in 45 minutes that requires 72 hours in a conventional drying oven.

Note.—Approved for publication April 13, 1965.

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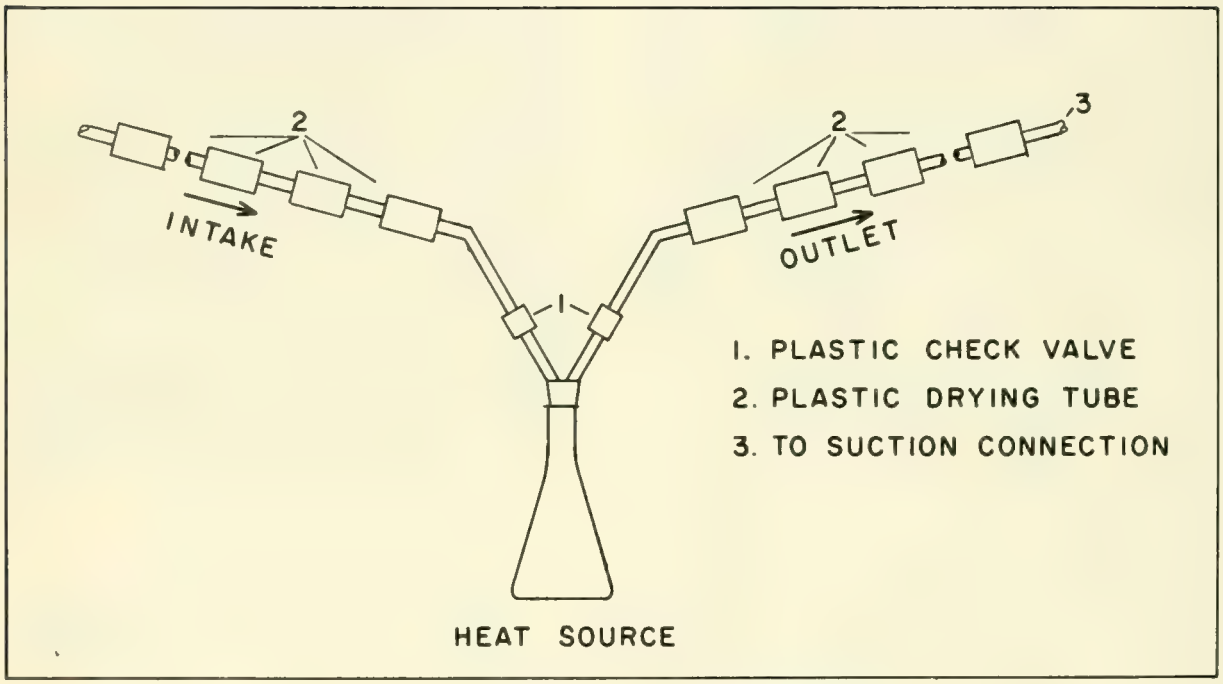

FIGURE 1.—Diagram of extraction apparatus.

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MARINE DECAPOD CRUSTACEANS of the CAROLINAS

Austin B. Williams

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